Dissolved oxygen as a constraint for the structure of mangrove fish assemblages and their patterns of mangrove utilisation: a comparison between natural and disturbed mangrove ecosystems through the Australian and Caledonian coastlines.

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Intellectual support	• Drafts review • Editing • Statistical support • Laboratory analyses design	• Prof Marcus Sheaves, Dr Nathan Waltham, Prof Cyril Marchand, Dr Ronald Baker, Dr Geoffrey Collins, Dr Martino Malerba • Eric Fakan, Jake Edmiston, Peter Gatenby • Dr Martino Malerba, Michael Bradley, Cesar Herrera, Dr Carlo Mattone • Prof Guy Claireaux, Dr Geoffrey Collins, Dr Jodie Rummer
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Abstract

Mangroves are commonly recognised as important fish habitats. However, studies that have quantified their utilisation by fish often found contrasting results, supporting the contention that mangrove forests provide heterogeneous values. Mangroves are dynamic, fluctuating and challenging environments consequently inducing variability in mangrove fish assemblages. Our understanding on the factors contributing to this variability is still limited, but essential to manage and conserve these valuable and threatened habitats.

Tide has been identified as one of the key factors to explain variations in mangroves utilisation. Tide is responsible for many physical changes such as water depth, current, connectivity, but also chemical changes such as dissolved oxygen (DO), salinity, temperature and pH. Considering the numerous changes driven by tide, it is difficult to quantify their specific influence on fish assemblages, and as a result, their role and relative importance is not fully understood. The objective of this thesis was to provide new understanding on temporal and spatial variability in the use of intertidal mangrove habitats by fish in response to fluctuating environmental factors. I identified that the two major challenges that fauna face while using intertidal mangrove habitats are the total drainage at low tide inducing a risk of stranding, and hypoxic conditions that can lead to physiological stress and death. Consequently, the importance of depth, hypoxia, but also the nature of the mangrove habitat were principally investigated as evidence shows that they could be key factors determining mangrove utilisation.

To begin understanding how hypoxia can limit the utilisation of intertidal mangrove habitats, DO and depth loggers were deployed over several days and tidal cycles across a mangrove wetland innorth-east Australia (**Chapter 2**). I characterised the DO dynamics at a short-time scale (tidal and diel) and a fine spatial scale and I investigated the effects of tidal factors on DO fluctuations. I also determined potential risks from exposure to hypoxic events for fish occupying this wetland. Results showed that DO daily reached harmful and occasionally lethal levels, and therefore had the potential to temporarily limit the utilisation of this wetland by fish. I also identified that DO closely followed tidal fluctuations.

To extend our knowledge on variations in mangrove fish assemblages in relation to environmental fluctuations, I deployed underwater video cameras coupled with multi- parameter loggers (DO, depth, salinity, temperature). I sampled on the edge of, and 5 m inside (in-forest), an intertidal mangrove forest, New Caledonia, to identify whether these two major components of mangrove forests were used differently. **Chapter 3** showed that fish assemblages on the mangrove edge and in-forest were highly distinct, with most species observed on the edge and few species entering in-forest. Fish assemblages also varied temporally across tide, most likely explained by species-specific tidal migrations, highlighting that fish responded to one or several environmental factors fluctuating with tide. The most evident factor varying with tide, and that can trigger tidal migrations, is water depth as the mangrove forest becomes temporarily unavailable to fish. However, chapter 2 showed that DO and depth are highly correlated, and that DO can reach harmful levels in intertidal mangrove habitats. As depth and DO are two potentially

limiting factors that vary across tide, I attempted to disentangle their confounding effects in causing fish tidal variations. Depth was statistically identified as the factor with the highest predictive power in explaining variations in fish assemblages, with species preferentially accessing mangrove habitats at different depth ranges. However, DO also varied with tide in this mangrove forest, reaching harmful levels especially early in the morning at low tide (**Chapter 4**). DO was also statistically identified as a key factor explaining fish tidal variations, therefore, I further investigated how fish responded to DO fluctuations. I found that fish displayed species-specific variations in response to DO, apparently explained by differential behavioural avoidance thresholds. Indeed, three distinct groups of species were identified based on distinct preferences for DO with species recorded from 30 to 110 % saturation, species recorded from 50-110 % saturation, and species recorded from 70 to 110 % saturation. Thus, I hypothesised that species-specific responses to DO could be explained by differential tolerances to hypoxia.

I used the results from chapter 3 to design laboratory experiments and test for this hypothesis (**Chapter 5**). I selected four species displaying distinct preferences for DO and I determined their physiological tolerances to hypoxia using intermittent-flow respirometry during which I decreased DO in accordance to what I observed in the natural environment. Results showed a causality between species physiological tolerance to hypoxia and mangrove habitat utilisation in response to DO. They suggest that species able to withstand low DO use mangrove habitats more extensively than more sensitive species. Consequently, it is probable that being highly tolerant to hypoxia is a

required pre-condition to thrive in these extreme environments, which could help explaining the little use of some intertidal mangrove forests.

The present research highlights that mangrove forests utilisation is highly variable over space and time. Their utilisation varies spatially depending on which components of the mangrove forest are studied such as the edge or the in-forest. Intertidal mangroves utilisation also varies temporally as tide creates many changes that can constraint fish. This study especially provides important knowledge on how DO can impact fish communities by favouring highly tolerant species to hypoxia, and on the other hand exclude more sensitive species. This new information can help explain the contrasting results found in the literature concerning the utilisation of mangrove forests. For instance, the higher contribution of coral reef fish to the mangrove fish assemblages in the Caribbean compared to other regions of the Indo-Pacific could be due to a lower hypoxia tolerance among coral reef fish compared to intertidal mangrove species. This study shows that fish using mangroves can sometimes be living on the edge of oxygen limitations. In the view of further predicted human-caused oxygen decrease, it is crucial to address the gaps of knowledge concerning DO dynamics in mangrove habitats, and its impacts on fish populations. This can assist managers and policy makers to establish appropriate management and conservation plans to ensure the sustainability of mangrove habitats.

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Chapter 1 General introduction

1.1. Discrepancies around the value of mangroves as fish habitats

Mangroves are commonly identified as important fish habitats (Mumby et al., 2004; Nagelkerken et al., 2008). However, the extent to which mangrove habitats are used by fish is often unclear as studies show varying degrees of utilisation (Nagelkerken et al., 2001; Mumby et al., 2004; Faunce and Serafy, 2006; Barnes et al., 2012; Sheaves et al., 2016). For instance, mangrove fish richness is usually limited in intertidal forests of the Indo-West Pacific, with often only few taxa dominating the assemblage (Robertson and Duke, 1990; Dorenbosch et al., 2005; Barnes et al., 2012; Reis-Filho et al., 2016; Sheaves et al., 2016), and their use being restricted to the mangrove forest edge (Sheaves et al., 2016). On the other hand, in the Caribbean, studies often report a high contribution of reef fish species to mangrove fish assemblages and are observed on the edge and inside the forest (Mumby et al., 2004; Dorenbosch et al., 2007). The contention that mangroves are important fish habitats is often not evidence-based but generalised from one location in one part of the world to another in other parts of the world while supported by limited data demonstrating ecosystem equivalence (Sheaves, 2012). Consequently, the lack of detailed understanding about mangrove habitats utilisation create discrepancy around the value of mangrove habitats for fish that is important to address.

Part of this apparent discrepancy could be addressed by identifying the factors responsible for the variability in mangrove habitats utilisation (Beck et al., 2001). A recent meta-analysis identified that tidal amplitude is a critical factor to explain differences in fish assemblages among locations (Igulu et al., 2014). For instance, a higher use of mangroves by juvenile fish is observed in locations with a small tidal range compared to locations experiencing a high tidal range (Igulu et al., 2014). Tidal variations generate a range of constraints that can explain this pattern. In locations

experiencing high tidal ranges, ebbing tides lead to the drainage of mangrove habitats, temporarily limiting their utilisation (Sheaves, 2005; Unsworth et al., 2007; Baker et al., 2015). Tidal variations also induce rapid changes in environmental conditions such as salinity, temperature, water depth, and dissolved oxygen (DO), that can temporarily and/or permanently create unsuitable habitats for fish (Davis, 1988; Rountree and Able, 2007; Brady and Targett, 2013; Mattone and Sheaves, 2017). Indeed, during tidal connections, sediments chemistry can impact water column chemistry through pore water exchange (Bouillon et al., 2007; Li et al., 2009; Gleeson et al., 2013). In mangroves, sediments are enriched in organic matter and reduced compounds such as NH_3, H_2S, FeS_2, making them anoxic, acidic and toxic within a few centimetres (Marchand et al., 2011). During flooding tides, water infiltrates the sediments and then drains back to the water column at ebbing tide releasing pore water that is enriched in toxins, acidic and depleted of oxygen (Call et al., 2015; Leopold et al., 2017), creating a potentially harmful environment for organisms that could prevent their utilisation. Rapid and extreme decline in DO experienced in mangrove habitats is likely to be one of the key controlling factors of their utilisation by fish (Knight et al., 2013; Gedan et al., 2017; Mattone and Sheaves, 2017), but it has rarely been considered.

1.2. Dissolved oxygen: a key controlling factor

One of the main limiting factors modified during tidal fluctuations in mangrove habitats is the oxygen content. Oxygen is a fundamental water quality parameter for all aerobic organisms, including fish, that depend on oxygen to survive (Driedzic and Hochachka, 1978). In the atmosphere, oxygen is freely available, and therefore almost never limiting. However, solubility of oxygen in water is poor (Kramer, 1987), and diminishes as temperature and salinity increase (Garcia and Gordon, 1992). Consequently, free molecules of oxygen are scarce in tropical marine environments which has resulted in the development of efficient mechanisms among fish to overcome the perpetual challenge of acquiring oxygen (Kramer, 1987).

1.2.1 Dissolved oxygen cycle in mangrove habitats

Many aquatic environments present an even greater challenge in terms of acquiring oxygen as they experience naturally low DO events, explained by dynamic physico-chemical processes (Mandic and Regan, 2018). In shallow water environments, such as mangroves, DO is extremely variable but generally predictable, as it varies on a diel basis (D'Avanzo and Kremer, 1994; Tyler et al., 2009; Knight et al., 2013; Mattone and Sheaves, 2017). During the day the autotrophic production is usually higher than oxygen consumption, consequently, DO can reach super-saturated concentrations in the mid-afternoon (Tyler et al., 2009). During the night, plants and animals respire, consuming oxygen produced during the day, leading to low DO, or hypoxia, early in the morning (Kenney et al., 1988; D'Avanzo and Kremer, 1994). There are five major processes that can explain why hypoxia occurs periodically in mangrove habitats (Figure 1). First, high biological oxygen demand (BOD), as mangrove trees produce a large amount of litterfall consisting of dead leaves, dead roots and dead fruits. This litterfall accumulates on the bottom, accounting for most of the organic matter found in mangrove forests degraded by bacteria that consume oxygen (Tanaka and Choo, 2000; Alongi et al., 2004b; Dittmar et al., 2006; Bouillon et al., 2008). Second, high chemical oxygen demand (COD), as mangrove sediments are active biogeochemial reactors generating many complex oxygen-dependent chemical reactions (Froelich et al., 1979; Van Cappellen and Wang, 1996; Marchand et al., 2004; Marchand et al., 2011). Third, high biomass, as mangrove habitats shelter many organisms that consume oxygen to respire (Nagelkerken et al., 2008). Fourth, high water temperatures that reduce oxygen solubility as mangroves are tropical and sub-tropical environments, therefore they are located in areas where the temperature is high (Duke et al., 1998). Fifth, lack of re-aeration processes, as mangroves are often sheltered areas, with low impact waves and little wind (Woodroffe, 1992; Augustinus, 1995). Consequently, water movements are limited, reducing the exchange of oxygen

between the atmosphere and the water column, as well as the physical transfers of more oxygenated water masses from adjacent habitats (Butler and Burrows, 2007).

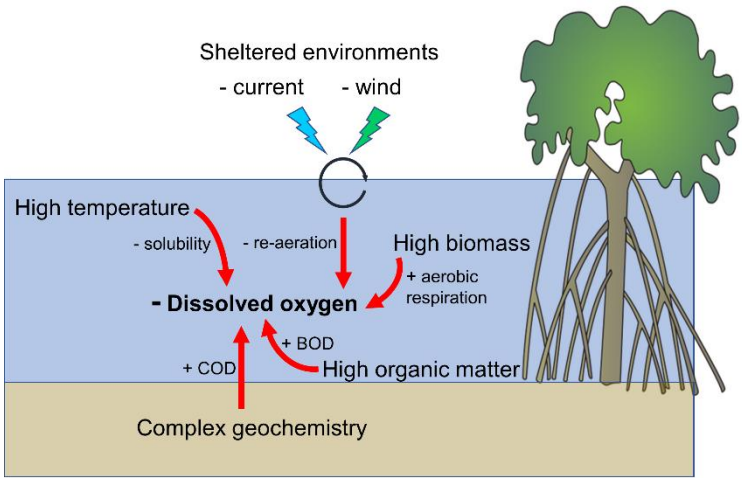

Figure 1 Processes responsible for naturally low dissolved oxygen conditions in mangrove habitats.

1.2.2 Impact of hypoxia on ecosystems functioning

The occurrence of hypoxia has important adverse effects on different organisational levels disrupting ecosystems functioning. On the individual level, hypoxia leads to changes in physiology and behaviour, affecting growth (Petersen and Pihl, 1995; Del Toro-Silva et al., 2008; Wang et al., 2009), reproduction (Wu, 2009; Wang et al., 2016), feeding (Pihl et al., 1991), and eventually survival (Ruggerone, 2000; Townsend and Edwards, 2003). Depending on the hypoxic severity and time of exposure, hypoxia has acute or sublethal effects on organisms. These effects on the individual level have larger scale effects on populations and communities (Chabot and Claireaux, 2008), such as reduced species biomass, individuals size, and genetic diversity (Wu, 2002; Eby et al., 2005a; Steckbauer et al., 2011), major changes in species composition (Dauer, 1993), functional groups (Diaz and Rosenberg, 1995) and predator-prey interactions (Breitburg et al., 1994; Breitburg et al., 1997). If hypoxia is severe and persistent, entire ecosystems can be temporarily or permanently lost (Rabalais et al., 2002; Diaz and Rosenberg, 2008; Levin et al., 2009). As low DO is an

critical stressor, it is expected that fish communities of hypoxic environments such as mangroves would be largely influenced by hypoxia occurrence and severity.

1.2.3 Specific adaptations to hypoxia

In response to the serious effects that hypoxia has on organisms, communities, populations and ultimately ecosystems, fish have developed specialised adaptations to tolerate and exploit hypoxic environments (Mandic and Regan, 2018). In intertidal environments experiencing rapid and severe changes in DO, such as mangroves, these strategies involve behavioural and physiological adaptations to enhance oxygen extraction and tissue delivery to sustain aerobic ATP production (Fry, 1971; Claireaux and Chabot, 2016; Mandic and Regan, 2018). Fish are mobile organisms and most likely able to sense oxygen changes (Das and Stickle, 1994; Claireaux et al., 1995; Schurmann et al., 1998; Wannamaker and Rice, 2000), thus, the first behavioural adaptation often involves temporal or permanent avoidance of hypoxic zones (Pihl et al., 1991; Brady and Targett, 2013). Fish able to withstand environmental hypoxia can perform other behavioural adaptations such as aquatic surface respiration (Kramer and McClure, 1982) or air-gulping (Burggren, 1982; McNeil and Closs, 2007). Fish also present physiological adaptations such as extended gill surface area (Nilsson, 2007), increased number of red cells (Wu, 2002) or higher oxygen binding capacity of haemoglobin (Craig et al., 2014). If the strategies to sustain aerobic ATP production listed above are not sufficient, fish can reduce energetic demands by suppressing non-vital activities such as swimming, feeding, growth and reproduction, referred to as metabolic rate depression (Wu, 2002; Richards, 2009). Ultimately, fish can resort to anaerobic pathways to enhance energy production to maintain life-sustaining activities and survive (Kramer, 1987; Chabot and Claireaux, 2008). These strategies enhance hypoxia tolerance but come at a cost influencing how and to which extent species resort to these adaptations to use hypoxic environments (Mandic and Regan, 2018). The wide range of hypoxia tolerance strategies developed by fish lead to species-

specific tolerances controlling hypoxic environments utilisation (Hilton et al., 2008; Vaquer-Sunyer and Duarte, 2008; Mandic and Regan, 2018). It is expected that fish living in mangrove habitats have developed species-specific adaptations to deal with oxygen vagaries, making them more or less susceptible to hypoxia, and therefore shaping mangrove fish assemblages.

1.2.4 Estimating the impact of hypoxia on ecosystem functioning

Ecological patterns, such as species distribution or migrations, in response to hypoxia are difficult to interpret as organisms usually face multiple stressors in the environment that can alter their responses (Vaquer-Sunyer and Duarte, 2008; Breitburg et al., 2018). An effective way of establishing a link between observed ecological patterns and environmental hypoxia is to assess species hypoxia tolerance using a common performance currency among aerobic organisms such as metabolism performance (McGill et al., 2006; Killen et al., 2013). Metabolism is the ensemble of chemical reactions needed to transform food material, or stored reserve, into energy (ATP) needed to fulfil activities (Chabot et al., 2016a; Nelson, 2016). Species' metabolism performance is related to their capacity to tolerate environmental hypoxia and therefore can explain patterns of hypoxic environments utilisation (Mandic et al., 2009; Killen et al., 2013). As oxygen acts as a final electron acceptor in the transport chain of aerobic respiration to produce ATP, and represents the most efficient pathway to acquire energy, physiologists have used oxygen consumption rate (O_2) as a proxy of metabolism performance (Chabot et al., 2016b).

O_2 can be monitored using special techniques called respirometry. The most accurate to monitor metabolism is intermittent-flow respirometry, described below according to Svendsen et al. (2015), that I used during this thesis (Figure 2). This technique consists of placing a fish in a metabolic chamber and measuring the decrease in oxygen concentration over time induced by respiration inside the chamber. To do so, the metabolic chamber is connected to a flush pump and a recirculation

pump. Alternatively, the chamber is sealed by stopping the flush pump in order to measure O_2 induced by the individual, and then opened by turning the flush pump on to renew the water, replenish the oxygen, and flush away wastes. A recirculation pump is fitted on a recirculation loop to assure water homogenisation inside the chamber. On the recirculation loop, an oxygen electrode is connected to a computer-controlled optical oxygen meter (firesting) via a fiber optic cable. It allows continuous oxygen measurements.

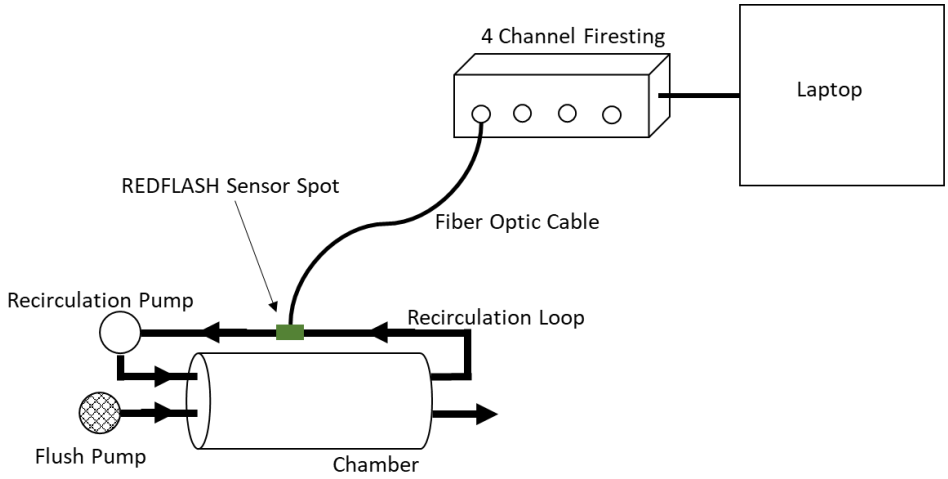

Figure 2 Intermittent-flow respirometry design.
The oxygen concentration (% saturation) is measured via a REDFLASH sensor spot adhered to the inside of the recirculation loop, which is connected to a four channel Firesting Optical Oxygen Meter via a fiber optic cable. The chamber is connected to two submersible pumps: a flush pump and a recirculation pump.

A set of metabolic measures quantifying hypoxia tolerance can be estimated with intermittent-flow respirometry while inducing a O_2 decline that will cause a gradual decrease in fish metabolic rate (Claireaux and Chabot, 2016) (Figure 3): 1) maximum metabolic rate (MMR) that represents the maximum energy available to support activities; 2) standard metabolic rate (SMR) that represents the minimum energy for the subsistence of an organism; 3) aerobic scope (AS) that represents the total energy available to perform aerobic activities; 4) the critical oxygen level (O_{2crit}) that represents the acute hypoxia tolerance below which vital maintenance cannot be sustained, compromising survival; 5) incipient lethal oxygen (ILO) level that represents the imminent-death hypoxia threshold at which a fish often loses its equilibrium (loss of

equilibrium: LOE) due to the accumulation of wastes following anaerobic ATP production; 6) time to LOE (time) that represents the amount of time spent in hypoxia between O_{2crit} and LOE; and 7) index of cumulative ambient oxygen deficit ($O_{2deficit}$) that represents the amount of O_2 consumed below O_{2crit} until LOE to assess resistance to hypoxia (Claireaux and Chabot, 2016). O_{2crit}, LOE, time to LOE and $O_{2deficit}$ are ideally determined by inducing a O_2 decline that is ecologically relevant, meaning that it reproduces "real-life" conditions that fish can experience in the environment. This facilitates the application of the knowledge obtained at an individual scale to the population level to allow a holistic approach. Therefore, it is important that laboratory experiments are combined with field data, which is rarely the case in the literature.

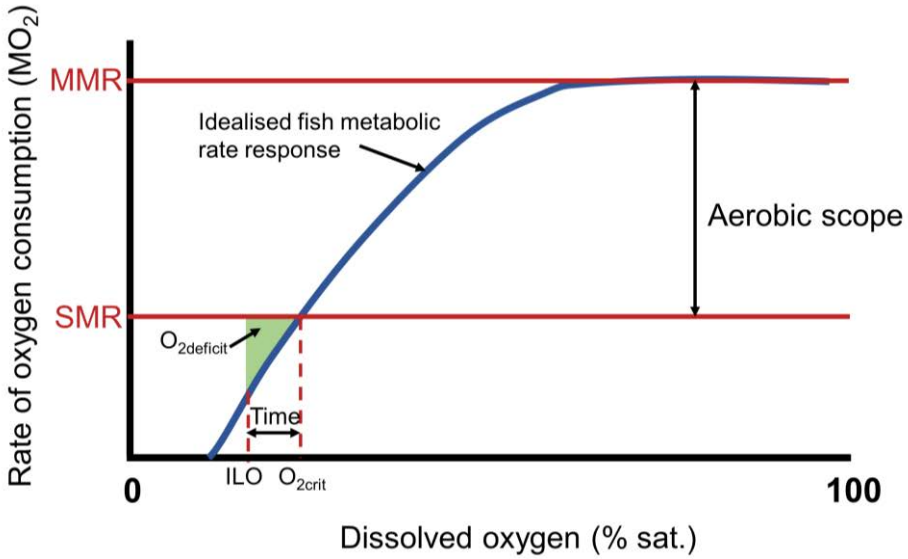

Figure 3 Influence of ambient oxygen decline on the metabolism of an idealised fish individual. MMR: maximum metabolic rate; SMR: standard metabolic rate; O_{2crit}: critical oxygen level; ILO: incipient lethal oxygen level; $O_{2deficit}$: index of cumulative ambient oxygen deficit.

1.3. Summary of knowledge gaps and thesis objectives

Discrepancies around the function and value of mangrove habitats among locations highlight the need for more explicit and detailed studies to characterise mangroves utilisation by fish. Mangroves are challenging environments, however, there is still little information on which factors influence or limit their value and utilisation. Tide is unarguably a key factor in influencing fish populations in intertidal

systems as it drives physico-chemical changes that make mangrove habitats temporarily inaccessible and unsuitable. Among changes caused by tide, DO is one of the most crucial as it is a key controlling factor of ecosystem functioning. Two recent studies have shown that DO can reach harmful levels in mangrove habitats, partly explained by tidal fluctuations (Knight et al., 2013; Mattone and Sheaves, 2017). These results support the idea that local DO conditions could be a key limiting factor to the value and use of intertidal mangrove habitats. However, this hypothesis has not been adequately investigated. While it is known that mangrove habitats can suffer from temporal hypoxia, it is not clear whether hypoxia is a common and widespread condition across different locations. The impact of hypoxia on mangrove fish communities is also largely unknown even though hypoxia is a strong selective factor in determining use of habitats. Concurrently investigating short-scale variations in DO and fish assemblages, and combining this field knowledge with physiological laboratory experiments to establish a link between hypoxia and observed ecological patterns is needed to investigate the potential of hypoxia to limit mangroves utilisation by fish.

The overarching aim of this thesis was to assess the role and importance of tidal fluctuations in environmental factors, especially DO, in influencing mangrove habitats utilisation by fish using field and experimental studies. The first aim of this thesis was to better understand DO fluctuations in intertidal mangrove habitats and answer specific questions such as how low does DO get, how often does hypoxia occur, and what is the role of tide in driving these fluctuations (Chapter 2). The second aim was to characterise and assess the role of tidal fluctuations in short-scale spatial and temporal variations in fish assemblages in intertidal mangrove habitats (Chapter 3). The third aim was to assess fish responses to tidal variations in DO in intertidal mangrove habitats (Chapter 4). The fourth aim was to determine whether observed patterns of mangroves utilisation in response to fluctuating DO were linked to species hypoxia tolerance (Chapter 5).

Chapter 2 Extreme dissolved oxygen variability in urbanised tropical wetlands: the need for detailed monitoring to protect nursery ground values

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2.1. Introduction

Unprecedented expansion of urban and industrial development has led to coastal wetland destruction, water quality degradation, and loss of biodiversity (Ehrenfeld, 2000; Roy et al., 2003; Argent and Carline, 2004). The remaining coastal wetlands suffer from a range of anthropogenic pressures (Lee et al., 2006), among which increased nutrient and organic matter loading, contributing to eutrophication, is one of the most important (Rosenberg, 1985). Severe and persistent hypoxia is a notable consequence of eutrophication (Nixon, 1995), and nowadays the increase in occurrence and severity of hypoxia are regularly reported in coastal waters because of continued eutrophication.

In shallow water habitats, such as coastal wetlands, diel-cycling hypoxia is common (Smith and Able, 2003; Knight et al., 2013), due to shorter, marked, dissolved oxygen (DO) fluctuations compared to subtidal areas (Kenney et al., 1988). Some aspects of diel-cycling DO are predictable, with lowest values occurring early in the morning (following night time respiration) and maximum values in the afternoon, following transition to photosynthesis (Mazda et al., 1990; D'Avanzo and Kremer, 1994; Tyler et al., 2009). These diel fluctuations are the result of a net difference between DO supply (photosynthesis, diffusion, tidal exchange) and consumption (biological oxygen demand, chemical oxygen demand). The amplitude of this cycling is influenced by environmental parameters such as solar radiation, salinity, temperature, wind

velocity, depth and tide (Mazda et al., 1990; Mandal et al., 2012; Baumann et al., 2015). In eutrophic coastal wetlands, amplitude is higher (Bouillon et al., 2008), and hypoxia becomes more severe, intensifying in occurrence and duration, which in turn, further increases exposure risks for organisms occupying these habitats (Breitburg 1992).

Low DO availability leads to perturbations in the bio-chemical dynamics of ecosystems, as many chemical reactions require oxygen (Hull et al., 2000; Hunt and Christiansen, 2000), and all aerobic organisms depend on oxygen for survival (Falkowski and Raven, 1997). Low DO has been linked to reduced growth (Del Toro-Silva et al., 2008; Stierhoff et al., 2009), impaired reproduction (Ruggerone, 2000; Dantas et al., 2012), diet alteration (Pihl, 1994; Zambonino-Infante et al., 2017), modified predator-prey interactions (Breitburg et al., 1994), shifts in distribution (Pihl et al., 1991; Breitburg, 1992), and altered community dynamics of marine animals (Wu, 2002).

Despite increasing coastal eutrophication (Breitburg, 2002) and the pressing need to monitor and limit the impact of hypoxia on aquatic fauna, there is surprisingly little information on DO dynamics for coastal wetlands (Knight et al., 2013), and particularly so in the tropics. Moreover, there is no agreed methodology to monitor DO or to examine the exposure risks to local aquatic fauna. Water quality monitoring programs in estuaries have typically adopted spot measurements. However, these data only represent a static point in time, which is likely to provide an incomplete representation of a dynamic parameter such as DO (Kerr et al., 2013).

To provide information on DO levels fish typically need to deal with daily in urbanised tropical wetlands, this study examines the fine temporal (15 minutes) and spatial (~50 m) scale DO fluctuations in an urbanised tropical coastal wetland typically found along the Great Barrier Reef (GBR) coastline in northern Queensland, Australia (Sheaves et al., 2007a; Waltham and Sheaves, 2015). Despite the potential impact of urbanisation on water quality, especially DO, this wetland functions as an important

regional nursery ground for invertebrates and fish (Sheaves et al., 2007a; Davis et al., 2012; Davis et al., 2014b). The objectives of my research were to: 1) characterise the DO dynamics at a short-time scale (tidal and diel) and a fine spatial scale; 2) investigate the effects of time of day and tidal factors on DO variability; 3) determine potential exposure risks to hypoxic events for fish occupying this tropical urbanised wetland; 4) provide some insights to develop meaningful DO monitoring programs to implement appropriate management and policies.

2.2. Materials and Methods

2.2.1 Study site

The study was conducted in Annandale Wetland, Ross River (19.19°S; 146.44°E), Townsville City, North Queensland, Australia (Figure 4). The region experiences meso-tidal and mixed semidiurnal tidal cycles (2 high tides and 2 low tides of different size each day). Annandale Wetland comprises an area of 0.4 km^2 dominated by *Sporobolous virginicus* saltmarsh and *Aegiceras corniculatum / Rhizophora stylosa / Avicennia marina / Ceriops tagal* mangroves (Davis et al., 2012). Annandale Wetland comprises more than 20 semi-permanent pools that range in size from 80 m^2 to 2,500 m^2, and in depth from 30 cm to 130 cm at low tide. These tidal pools vary from freshwater during the austral wet season, to saltwater in the dry season. They are connected to Ross River via a network of channels ranging between 0.5 m to 10 m in width. During spring tides, pools get connected (at high tide) with the adjacent Ross River, renewing remaining water. The disconnected time depends on the pool elevation but was never too long concerning the selected pools as enough water remained in the pools throughout the study, providing potential temporal refuges for fish.

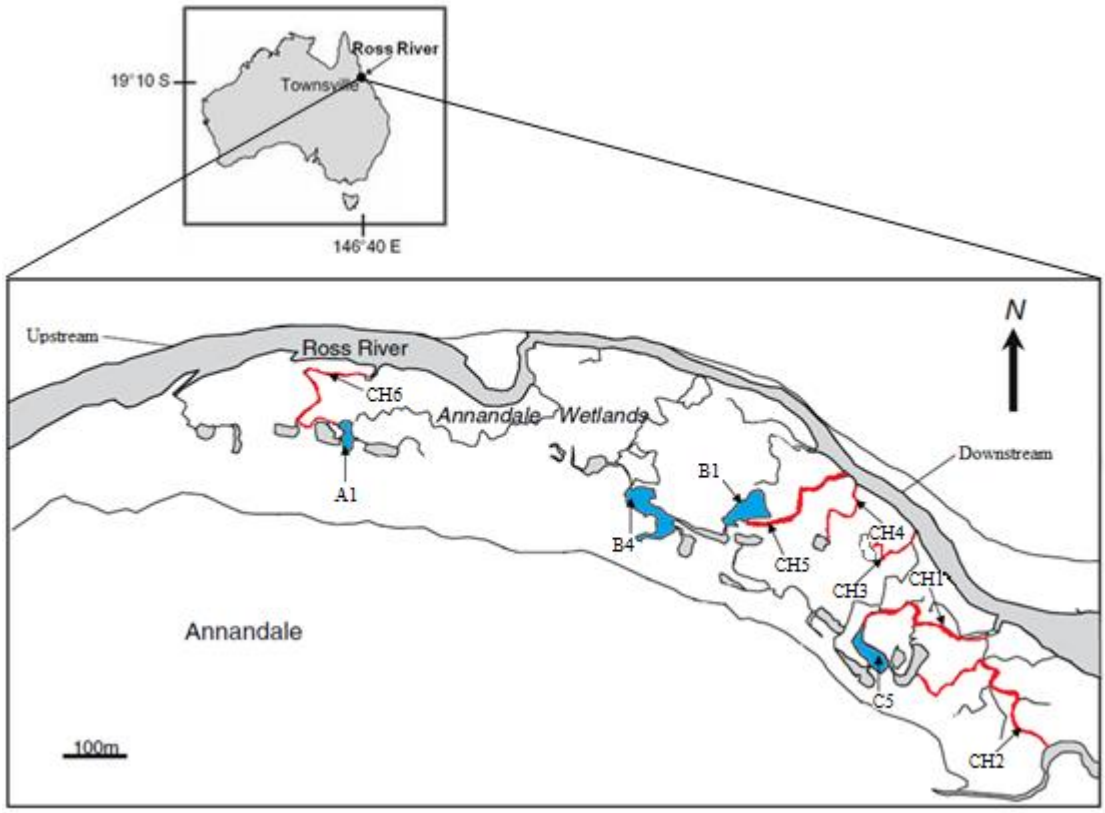

Figure 4 Map of the study site Annandale Wetland, Townsville, North Queensland, Australia. It comprises the 6 channels (CH1, CH2, CH3, CH4, CH5, CH6), highlighted in red, and the 4 pools (C5, B1, B4, A1), highlighted in blue, sampled between the 26th of January and the 23rd of March 2014.

Pools differ in terms of extent and density of fringing mangrove (a dense, almost complete fringe in downstream pools, grading to sparse, incomplete fringes in upstream pools), in sediment composition (fine mud, through coarse sand, to cobble), and in positioning relative to the Ross River (Figure 4). In this study, four tidal pools were selected: C5 (area: 1,020 m^2), B1 (area: 2,550 m^2), B4 (area: 2,800 m^2), A1 (area: 1,130 m^2) (pool names used here are the same reported in Davis et al. (2014a)). Six connecting channels were also selected, three directly connecting the study pools and the Ross River: CH6 (5 m width), CH5 (6 m width), CH1 (3 m width), and three other channels leading to pools that were not studied: CH2 (2 m width), CH3 (1 m width), CH4 (1 m width). The 10 locations were situated within 1.3 km range, with a minimum distance of 50 m between sites.

2.2.2 Data collection

Water column dissolved oxygen (DO) sampling was conducted over seven campaigns between January and March 2014 at 10 locations within the wetland, representing between 3 and 10 days of sampling at each of the 10 locations (Table 1).

Table 1 Summary of the sampling periods.
They were conducted between the 26th of January 2014 and the 23rd of March 2014 at ten different locations in Annandale Wetland in Townsville. For each location, the number of days sampled is indicated, along with the dates of the different sampling periods. For each sampling period and sampled location, the minimum and maximum values recorded for DO, temperature and tidal range are provided, as well as the total rainfall.

Location	Number of days sampled	Sampling periods	Min and max DO (% sat)	Min and max temperature (°C)	Rainfall (mm)	Min and max tidal range (m)
CH1 (downstream-upstream)	10	26-28/01/14	54.31-139.38	24.2-33.9	21.80	1.2-2.5
		03-06/02/14	19.25-178.91	24.0-31.3	10.00	0.6-2.4
		11-13/03/14	43.04-120.88	22.6-32.3	0.00	1.4-2.3
CH2 (downstream-upstream)	7	10-11/02/14	48.60-98.90	25.2-30.8	23.40	1.3-2.4
		03-07/03/14	55.48-86.61	23.9-29.2	3.40	0.5-2.7
CH3 (downstream-upstream)	7	10-11/02/14	42.59-123.77	26.0-33.4	23.40	1.3-2.4
		03-07/03/14	3.75-117.39	23.9-32.0	3.40	0.5-2.7
CH4 (downstream-upstream)	7	10-11/02/14	42.45-141.24	26.4-35.3	23.40	1.3-2.4
		03-07/03/14	44.16-145.86	23.8-33.1	3.40	0.5-2.7
CH5 (downstream-upstream)	3	11-13/03/14	54.09-97.51	25.7-29.0	0.0	1.4-2.3
CH6 (downstream-upstream)	3	11-13/03/14	44.96-142.55	22.6-31.9	0.0	1.4-2.3
C5	8	14-16/03/14	13.06-92.05	24.2-31.2	0.0	1.7-2.3
		19-23/03/14	15.08-102.40	24.0-28.9	65.8	0.4-1.9
B1	8	14-16/03/14	27.38-101.34	23.3-31	0.0	1.7-2.3
		19-23/03/14	15.88-134.75	23.2-31.8	65.8	0.4-1.9
B4	8	14-16/03/14	18.15-136.08	23.0-33.3	0.0	1.7-2.3
		19-23/03/14	53.16-145.71	23.9-36.0	65.8	0.4-1.9

A1	8	14-16/03/14	49.44-128.44	26.3-32.5	0.0	1.7-2.3
		19-23/03/14	19.58-160.35	25.2-32.0	65.8	0.4-1.9

Near-bottom (around 5 cm above the sediment) DO, water temperature, and atmospheric pressure in the four pools and the six channels were undertaken using multi-parameter probes (YSI Pro ODO model (accuracy ± 1% saturation)). In each pool, a single logger was deployed on the edge as far as possible from the mouth of the supplying channel. To link diel DO-cycling with tidal fluctuations, the probes were coupled with depth loggers (In-Situ Inc. Rugged Troll 100 model), which recorded total pressure every 15 minutes. Total pressure values recorded on the depth loggers were corrected for atmospheric pressure recorded with the YSI loggers to provide a record of water depth with approximately 5 cm accuracy. The YSI loggers were programmed to log every 5 minutes across the tidal cycle. To avoid calibration drift and fouling, probes were calibrated before and after each sampling campaign, however no drift was recorded. Photosynthetically Active Radiation (PAR) data were obtained from the nearby (27 km away) Australian Institute of Marine Science (AIMS) automatic weather station (Licor LI-192SA Quantum Sensor) site Cleveland Bay (19° 09.35S, 146°52.87E) from the 26 January to the 23 March 2014. Tidal range data for the general area were obtained with the official software AusTides 2014 provided by the Australian Hydrographic Service. DO data were omitted when water column depth was less than 5cm as probes were exposed to air.

2.2.3 Data analysis

All sites showed a non-linear trend in DO throughout the day that consistently peaked during the late afternoon, and declined at night, reaching minimum DO in the early morning. This non-linear trend is believed to be driven by photosynthesis activity affected by the rate of photosynthetically active radiations available, and respiration. As these biological processes follow a diel-cycle, time of day was used as a proxy to account for the diel-cycling DO. A model was built to subtract the diel-cycle trend from DO values. Therefore, a General Additive Mixed Model with a cubic spline smoother (GAMM) was used, with data grouped into 60-minute intervals for each site. The dependent variable was nested within the sampled sites. Hence, a random intercept was included for each site to account for the nested experimental design.

Overall, the model consisted of DO (% saturation) as the dependent variable, and two independent variables for hour of day (0 being midnight) (fixed effect) and sites (random effect). The analysis was completed using the package “mgcv” in R statistical software, fitted with Maximum-Likelihood techniques (Wood, 2011; R Core Team, 2014). The degree of smoothing in the GAMM was optimised with ordinary cross validation by minimising the mean-squared prediction error.

Residuals were obtained from the previous model. They represent DO values free from any diel-cycle pattern, called time-corrected values for DO (tcDO). This step was necessary as the strong diel-cycle pattern observed could hide the effects of other factors such as tidal factors. To develop an understanding of the effect of tidal factors on DO, the residuals from the GAMM were analysed as the response variable in a linear mixed-effects model (LME) using the R package “lme” (Pinheiro et al., 2015). As tidal connectivity is complex, given tides continually change, the best characterisation was to use the four different factors: tidal range, water depth, tidal direction, and water velocity, to capture most of the variation to better understand the influence of tidal connectivity on high frequency DO dynamics. Therefore, the model consisted of ten fixed effects including four main effects (three continuous: tidal range (m), water depth (cm), tidal velocity ($cm.min^{-1}$); one categorical: tidal direction (i.e. increasing or decreasing)) and all combinations of two-way interactions. Standardised (beta) coefficients were calculated in the LME to evaluate the relative effect on DO of each term in the model by standardising all continuous variables (i.e. subtracting the mean and divide by the standard deviation). As for the GAMM, a random intercept for each site was included in the LME to account for the nested experimental design. The suitability of the model was validated by ensuring low collinearity between main effects (i.e. variance inflation factor less than 5 (Zuur et al., 2009)), and that there were no systematic trends between normalised residuals and each of the covariates. In these data, the factors “water velocity” and “tidal range” were positively correlated, (variance inflation factor of 5.13), and could not be both included as explanatory factors in the same model. Water velocity was calculated from the rate of change of the water depth and so, not considered as accurate as the tidal range given by the

Australian Hydrographic Service. Thus, water velocity was removed from the model, reducing the maximum variance inflation factor score to 2.82, which was below the assumed cut-off value of 5. Because heteroscedasticity was detected in the LME between sites, different variance coefficients were included for each site in the LME variance structure. A cumulative frequency plot was used to determine the occurrence of the different threshold of DO in each site. The data used for this plot were the 60-minutes mean values of DO for each site.

2.3. Results

2.3.1 Dissolved oxygen patterns

More than 1,152 hours of DO data were recorded, consisting of 360 hours of data from tidal pools, and 792 hours from channels, with 384 hours recorded during increasing tides and 768 hours during decreasing tides. The maximum DO % saturation reached was 178.91 % saturation, while the minimum was 3.75 % saturation (Table 1).

Daily changes in DO saturation showed qualitatively consistent dynamics across sites: minimum values were recorded in the early morning between 3am and 6am, while maximum values were recorded between 2pm and 6pm (Figure 5). Magnitudes in DO saturation varied from site to site, highlighting a high spatial variability within this small-scale wetland. For instance, CH3 was the only case where DO saturation was close to zero for consecutive hours (< 5 % saturation), while DO saturation at other sites ranged between 13 % saturation and > 100 % saturation (Figure 5).

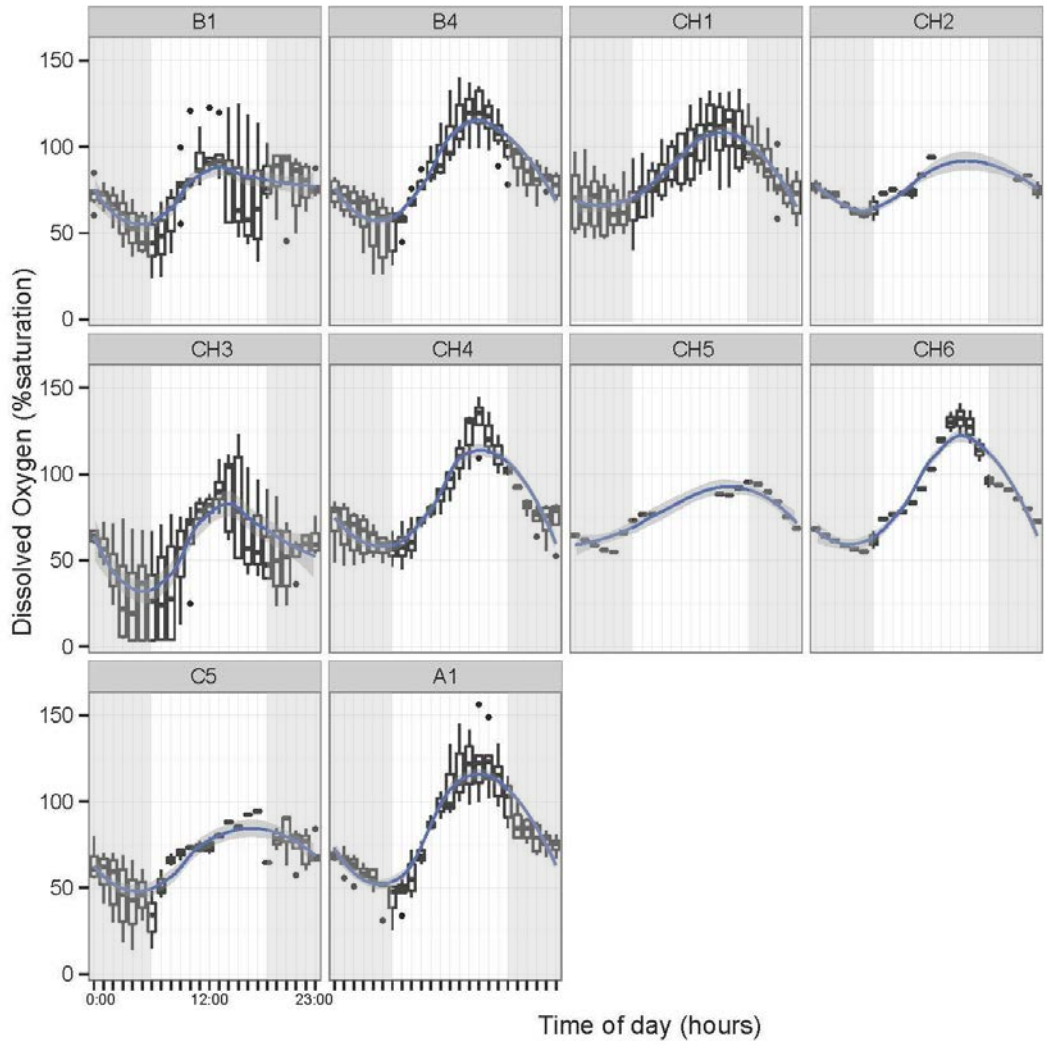

Figure 5 Boxplot of the 60 minutes means of DO (% saturation) across time of day for each site. Sites were sampled in Annandale Wetland from the 26th of January 2014 to the 23rd of March 2014. The blue line represents the model fitted for each site (generalized additive mixed model with a cubic spline smoother 60 minutes definition) to model the DO trend during a daily cycle. Shaded areas represent sunset to sunrise.

The cumulative distributions for DO showed consistent trends across sites, with highest densities mostly between 50 % saturation and 100 % saturation (Figure 6). In this study, DO below 50 % saturation was considered harmful, and was therefore selected as the threshold for hypoxia (Breitburg, 2002; Perna and Burrows, 2005). In this study, more than 118 h of low DO (≤ 50 % saturation) were recorded every day at 7 out of 10 sites (CH1, CH3, CH4, A1, B1, B4, C5), which represented a probability of approximately 0.11 of hypoxia (Figure 6). Around 80 % of low DO concentrations occurred between 1am and 11am, with approximately 60 % between 5am and 11am. Spatial variability was also evident, as the

locations experienced different probabilities for low DO or supersaturated DO. For instance, site CH3 showed a higher probability (around 0.41) for low DO (Figure 6). There was an overall probability of 0.2 of supersaturated DO observed at 7 of the 10 sites (Figure 6).

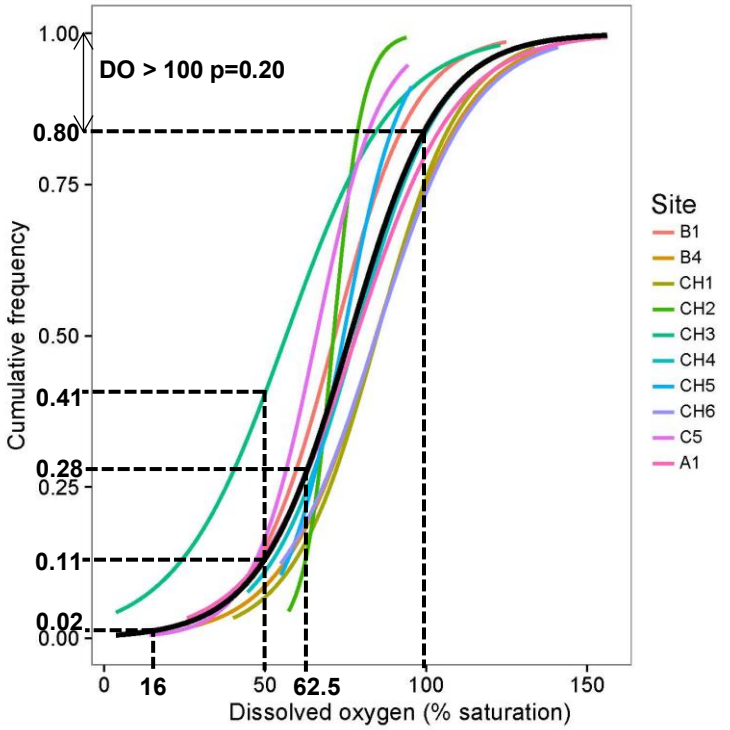

Figure 6 Cumulative frequency distribution of the 60 minutes means of DO (% saturation) across the ten sites.
Sites were sampled in Annandale Wetland from the 26th of January 2014 to the 23rd of March 2014. Each coloured line corresponds to a unique site among the ten sites sampled. The black line indicates the mean cumulative frequency of DO across all the sites. The dashed lines represent the ATV (Acute Trigger Value; 16 % saturation) and CTV (Chronic Trigger Value; 62.5 % saturation) for barramundi, the probabilities for low DO across all sites and for site CH3, and the probability for over-saturated values (1-0.8=0.2).

2.3.2 Drivers of dissolved oxygen variability

There was a strong correlation between increasing DO and the increase in PAR beginning at sunrise (Figure 7). Peak DO was recorded between two and four hours after peak PAR, while minimum DO occurred between 9 to 13 hours after sunset (PAR reduced to zero; Figure 7).

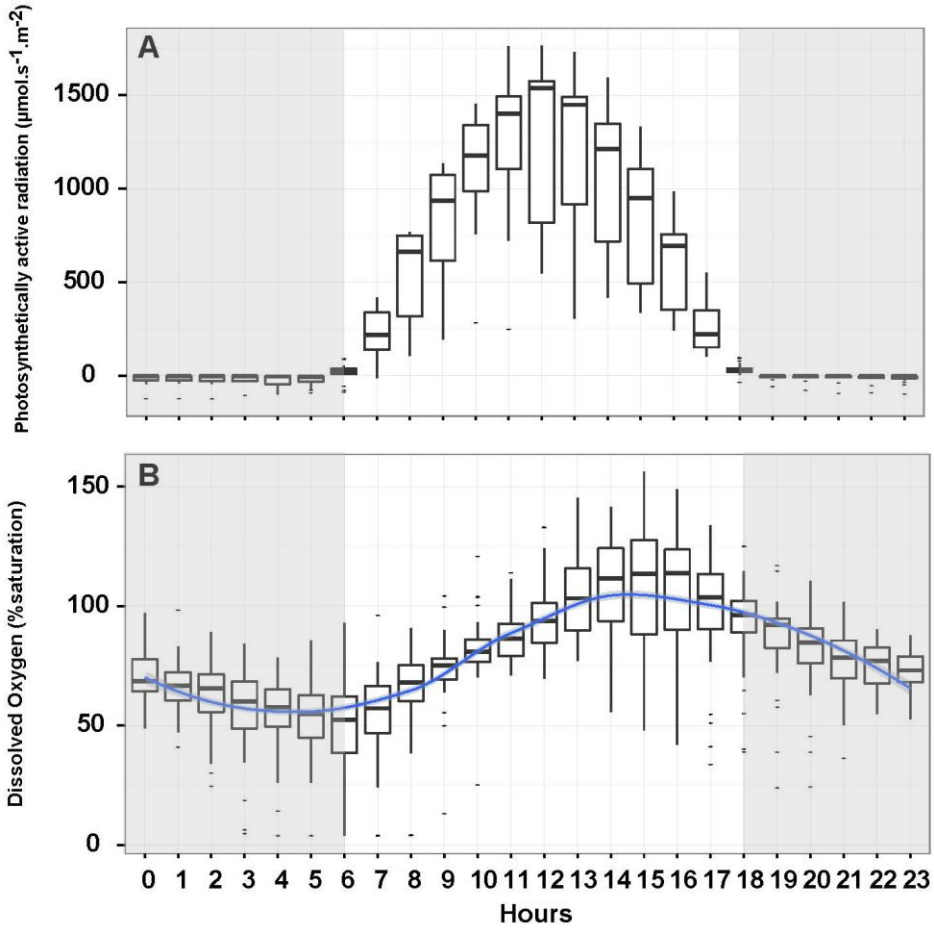

Figure 7 Boxplot of the 60 minutes means of (A) Photosynthetically Active Radiation (PAR) (µmol.s-1.m-2) and (B) DO (% saturation), across the diel-cycle (from 0=midnight).
Means were averaged across the ten sites sampled in Annandale Wetland from the 26th of January to the 23rd of March 2014. The blue line represents the model fitted (generalized additive mixed model (GAMM) with a cubic spline smoother 60 minutes definition averaged across all study sites) to model the DO trend during a daily cycle. The residuals (or time corrected values for DO (tcDO)) are scattered across this blue line. Shaded areas represent sunset to sunrise.

The GAMM accounted well for the non-linear daily patterns in DO ($F = 164.3$, $p < 0.001$, estimated degree of freedom of 7.83). The residuals from the GAMM represent time-corrected values for DO (tcDO). If the residual is on the blue line, the corresponding DO value follows perfectly the daily cycle model (GAMM); if the residual is below the blue line, the corresponding DO value is lower than the value predicted by the GAMM, probably because of other parameters that lowered the observed DO value; if the residual is above the blue line, the corresponding DO value is higher than the value predicted by the GAMM probably because of other parameters that increased the observed DO value. This strong diel-cycle

was hiding other potential DO variations. Therefore, these tcDO were used to identify whether other factors influenced DO fluctuations. LME highlighted that tcDO were significantly influenced by tidal range, water depth, direction of the tide (i.e. flood vs. ebb), and particularly by two two-way interactions between tidal range and water depth, and between tidal range and tidal direction (Table 2).

Table 2 ANOVA table for the linear mixed-effects model.

Variables	NumDF	DenDF	F-value	p-value
Intercept	1	873	0.32224	0.5704
Tidal range	**1**	**873**	**84.19963**	**<.0001**
Water depth	**1**	**873**	**90.72264**	**<.0001**
Direction	**1**	**873**	**8.63912**	**0.0034**
Tidal range:Water depth	**1**	**873**	**9.36286**	**0.0023**
Tidal range:Direction	**1**	**873**	**11.66720**	**0.0007**
Water depth:Direction	1	873	0.59173	0.4420

LME model was performed on the residuals from the GAMM (tcDO). This ANOVA tested the effect of the four main standardised fixed effects (three continuous: tidal range (m), water depth (cm), tidal velocity (cm.h^{-1}) and one categorical: tidal direction (i.e. increasing or decreasing)), and all combinations of two-way interactions between these four fixed effects on tcDO. The significant p-values are in bold letters.

tcDO decreased strongly with tidal range (Figure 8). This negative effect was dependent on the tidal direction, namely, if tide was ebbing or flooding (Figure 8). Indeed, during an ebb tide, the decrease of tcDO was greater than during a flood tide. Moreover, the model showed that the critical value of tidal range, above which tcDO became negative, was somewhat higher during a flood than an ebb tide.

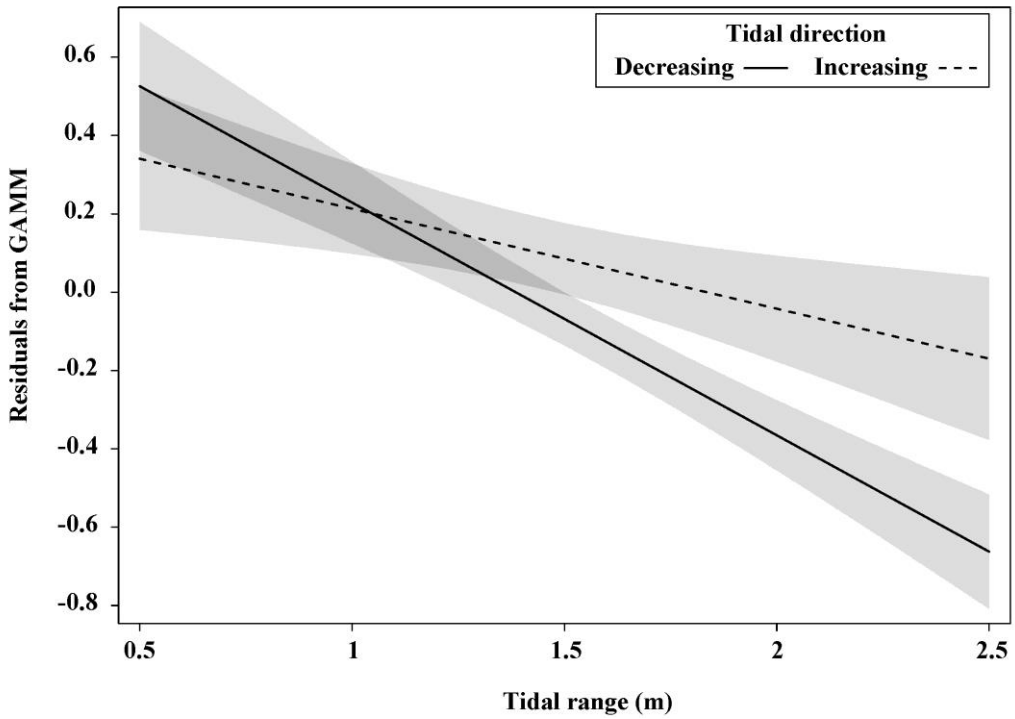

Figure 8 Significant effect of the two-way interaction between tidal range and tidal direction (i.e. flood or ebb) on the residuals from the GAMM (tcDO).
Effects were determined with a linear mixed-effects model that included ten fixed effects: four main effects (three continuous: tidal range (m), water depth (cm), tidal velocity (cm.h-1); one categorical: tidal direction (i.e. increasing or decreasing)) and all combinations of two-way interactions. The shaded areas represent the confidence interval at 95%.

tcDO increased with water depth (Figure 9). This relationship was dependent on tidal range (Figure 9). For small tidal ranges, the relationship was weak, however, above 1.5m the relationship improved, with the slope increasing across the tidal range. The maximum values of tcDO remained the same across the tidal range, but the minimum values of tcDO became more negative with the tidal range.

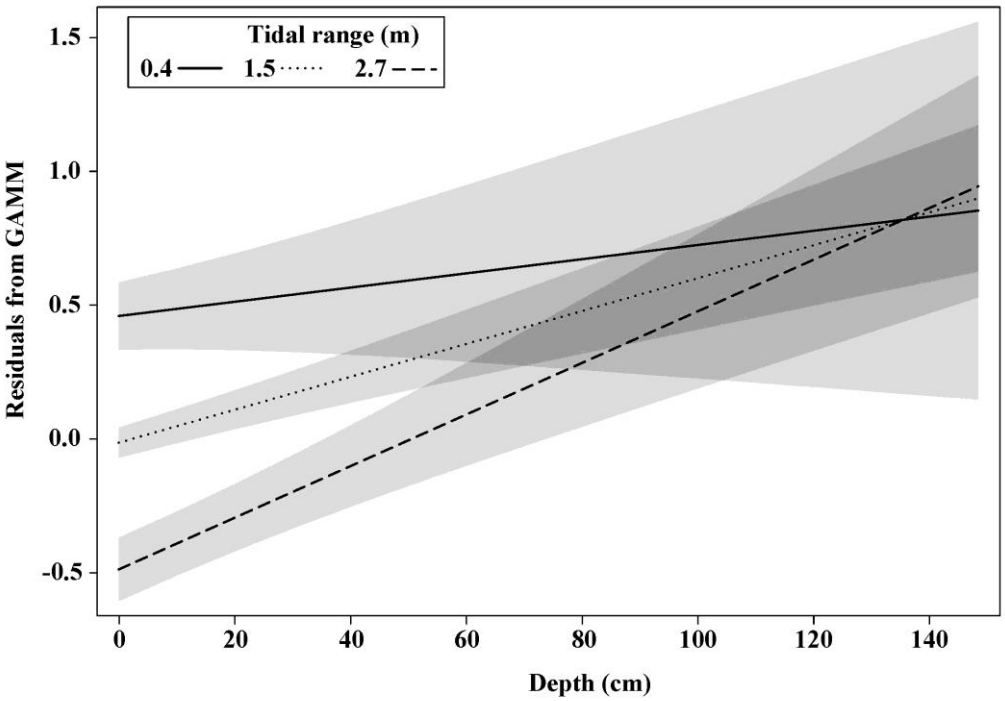

Figure 9 Significant effect of the two-way interaction between the water depth and the tidal range on the residuals from the GAMM.
Effects were determined with a linear mixed-effects model that included ten fixed effects: four main effects (three continuous: tidal range (m), water depth (cm), tidal velocity (cm.h-1); one categorical: tidal direction (i.e. increasing or decreasing)) and all combinations of two-way interactions. The shaded areas represent the confidence interval at 95%.

DO was extremely variable over time and space. The high spatial and temporal DO variability was primarily affected by time of day and tidal factors, namely water depth, tidal range and tidal direction. Early morning hours, high tidal ranges, ebbing tides, and low water depth were all factors that negatively affect DO. Temporal variability was mainly explained by time of day, related to the diel-cycle of PAR affecting photosynthesis processes, while spatial variability was mainly explained by the location of the study pools and channels in relation to Ross River. Hypoxia, including a single event when DO declined to almost 0 % saturation for consecutive hours, was recorded almost daily at 7 of the 10 study sites. Overall, a probability of 0.11 for hypoxia was recorded during this study.

2.4. Discussion

2.4.1 Dissolved oxygen temporal and spatial variability

Time of day was the main explanatory variable for temporal variability in DO saturation observed in pools and channels at the Annandale wetland. Changes in DO saturation closely followed the diel-cycle and were correlated with PAR, suggesting that photosynthesis was a major pathway of re-oxygenation. The high amplitude of DO measured over a 24h period characterises a habitat that is enriched in organic matter (Bouillon et al., 2008), a common occurrence in wetlands, as well as other shallow water and productive habitats such as estuaries, lakes, lagoons and mangroves (D'Avanzo and Kremer, 1994; Smith and Able, 2003; Tyler et al., 2009).

Tidal factors, especially tidal range, tidal direction (flood vs ebb), and water depth, were other key factors contributing to the temporal and spatial variability measured in this study. The tidal dynamics, representing a cycle of approximately 6 hours, determined temporal DO variations. As tidal pools and channels differ in their positioning relative to Ross River, tide did not influence them to equivalent extents, contributing to spatial variability observed among the locations.

The two-way interaction between tidal range and tidal direction had an important impact on tcDO, with tcDO decreasing as tidal range increased, the decrease being more important during ebbing tides. Spring tides can induce resuspension of sediments that can include sulfidic enriched sediments that consume DO (Nelson et al., 1994; Bush et al., 2004; Okamura et al., 2010). Low lying coastal wetlands located along eastern Australia, such as Annandale wetland, are likely to contain high concentrations of sulphides (Walker, 1972; Sammut et al., 1996), known as Potential Acid Sulfate Soils (PASS) (Alsemgeest et al., 2005). PASS are a particular problem where land is drained (White et al., 1997). When the PASS soils become oxidised, it creates severe and persistent hypoxia and acidification that can kill fish and crustaceans (Stumm and Morgan, 1981; Nelson et al., 1994; Bush et al., 2004). More data would be needed to determine whether past drainage works carried out in Annandale Wetland decades ago to increase tidal exchange and for mosquito control (Lukacs, 1996) play a role in determining the occurrence and extent of hypoxic events recorded here.

tcDO decrease across the tidal range was less marked during flood tides than ebb tides. During flood tides, it is likely that freshly oxygenated sea water enters the wetland (as it is suggested by the increase in tcDO with water depth), supplying channels and pools with DO, and offsetting potential tcDO decrease induced by oxygenation of resuspended sulfidic enriched sediments. Consequently, the process of freshly oxygenated sea water entering the wetland is likely to be important in the provision of nursery habitat for fish, particularly in a region of massive urban development and industrial expansion (Waltham and Sheaves, 2015).

The interaction between water depth and tidal range had a substantial impact on tcDO. tcDO were positively correlated with water depth, increasing during flood tides, and decreasing during ebb tides. In line with other studies conducted in tidal estuaries (Nezlin et al., 2009; Krumme et al., 2012; Knight et al., 2013), DO in Annandale Wetland varied with semi-diurnal tidal cycles. The relationship between tcDO and water depth was more apparent during spring tides. The amount of water flowing into the wetland with the tide was on average around three times less during neap tides than spring tides. Most of the wetland received little tidal exchange during neap tides, resulting in small tcDO changes across the tide. During spring tides, a greater tidal exchange seemed to deliver more freshly oxygenated water, leading to a consequent increase in tcDO across the tide. These results highlight that tidal connectivity, especially during spring tides, was an important process contributing to higher DO. Consequently, differences in tidal connectivity between the pools and channels (Davis et al., 2014a) is likely to be a contributor to the observed temporal and spatial heterogeneity in DO.

DO is likely to undergo seasonal changes as well. This study only considered DO over summer months, when extreme values of DO are most likely to occur because of high water temperature conditions in northern Queensland (Waltham & Sheaves 2017), increased freshwater inflow, and algal blooms (Gilbert et al. 1968; D'Avanzo & Kremer 1994; Nezlin et al. 2009). However, it is expected that DO dynamics would be different during the cooler dry season between June and August.

Clearly, DO dynamics of coastal tidal wetlands are complex, and depend on a range of biotic and abiotic conditions that vary at multiple spatial and temporal scales (Smith and Able, 2003). This variability highlights the need to use appropriate intensities of data collection to fully represent this complexity (Mazda et al., 1990; D'Autilia et al., 2004; Knight et al., 2013). This is particularly necessary in tropical coastal wetland areas that are important habitat for fish and invertebrates (Sheaves et al., 2007a; Davis et al., 2012). Obtaining high frequency water quality measurements for DO, and other parameters such as temperature (Wallace et al., 2015), is becoming increasingly viable with advances in technology and reducing costs of purchasing equipment, providing substantial information over the spot measurements that are unable to appropriately characterise variability and underlying processes.

2.4.2 Dissolved oxygen implications for fish

Fish use extensively salt-marsh tidal pools as temporal refuges or permanent habitats. However, exposure to low DO could be a constraint for the utilisation of these habitats by fish. The consequences of acute and chronic exposure effects to low DO on tropical estuarine fish in Australia is poorly known. The only Australian study available to compare here, is a study from Butler et al. (2007) and, while it focused on freshwater environments, the species investigated include a number of estuarine fish known to inhabit the Annandale wetland (Davis et al., 2012). Butler et al. (2007) presented two DO thresholds: 1) Chronic Trigger Value (CTV) - the limit for chronic exposure effects when fish start to increase gill ventilation rate, and 2) Acute Trigger Value (ATV) - the limit for acute exposure effects when fish are no longer able to increase gill ventilation rate to cope with lower DO values (Butler and Burrows, 2007). In the example here, barramundi (*Lates calcarifer*), an iconic and economically important species well distributed across northern Australia (James et al., 2017), recorded in Annandale Wetland, has an estimated ATV of 16 % saturation, and a CTV of 62.5 % saturation (temperature comprised between 23 and 33°C) (Butler and Burrows, 2007). In applying these thresholds, I determined exposure risks for barramundi using accumulative frequency curves (Figure 6). There was a probability of 0.02 for Barramundi to be exposed to acute effects

during the study logging time, and a probability of 0.28 that they would be exposed to chronic effects (Figure 6). Barramundi is a moderate-sensitive species and it is likely that more sensitive species inhabit this wetland, being more vulnerable to DO conditions recorded here. These results assume that the Annandale Wetland does not always provide optimum DO conditions for fish. More data should also be collected to study the DO dynamics in relation with fish utilisation of these tidal pools during the dry season, and assess if they represent a good seasonal refuge with sustainable DO levels.

Fish are known to have strategies to cope with low DO conditions. They can remain in poorly oxygenated waters by displaying physiological and behavioural adaptations such as air-gulping, aquatic surface respiration, and changing metabolism to conserve energy (Kramer, 1987; Wu, 2002; Flint et al., 2015). They can also avoid harmful DO conditions by either not using the poorly oxygenated areas, or by moving away from these areas during critical hours (Brady and Targett, 2013), for instance early morning in summertime at decreasing tide, highlighting the importance of wetland connectivity (Sheaves and Johnston, 2008). Exactly which of these adaption strategies are utilised by fish are not known and requires more detailed research. However, the utilisation of such strategies can certainly explain why Annandale Wetland is still a functional fish habitat despite the common occurrence of hypoxic events, and could play an important role in maintaining regional biodiversity.

There is still an on-going debate over the threshold for hypoxia that should be adopted, some authors arguing that the commonly used threshold (20 % saturation to 30 % saturation; (Vaquer-Sunyer and Duarte, 2008)) is not conservative enough (Breitburg, 2002; Vaquer-Sunyer and Duarte, 2008). This study highlights that even if realistic laboratory-determined thresholds were applied, fish would still be exposed to potential chronic and acute effects in these wetland habitats. However, fish still use extensively these habitats because they are adapted to these naturally-stressed environments (Elliott and Quintino, 2007). Considering the complex DO dynamics and adaptations by fish to cope with low DO conditions, it does not seem feasible to define a unique threshold for hypoxia, explaining the wide range of values

found in the literature. Rather than trying to determine a common agreed hypoxia threshold, more studies investigating exposure risks, especially chronic exposure effects, over a range of species, using standardised approaches combined with field studies at local or regional scales, should be undertaken for conservation purposes.

2.4.3 Management considerations

Measuring DO using high frequency loggers is probably more important than previously considered in the protection and management of coastal wetlands. I advocate here that DO should be measured at least every hour over a 24h cycle, across different tidal regimes, and across diverse types of habitats. Ideally, DO should be measured for an extended period that covers an entire tidal cycle (around 14 days), and across a fine spatial scale.

The high frequency data obtained during this study have important consequences when considering the applicability of water quality guidelines that aim to protect aquatic ecosystems. For instance, the Australian and New Zealand Guidelines for Fresh and Marine Water Quality (ANZECC/ARMCANZ, 2000) stipulate that DO in tropical Australian wetlands should not fall below 90 % saturation. Clearly this threshold is exceeded, and for many hours of the day, in the study wetland. However, the high abundance of fish recorded in this wetland suggests that they are adapted to deal with vagaries of diel hypoxia as highlighted in this study, and therefore, it cannot be assumed that normoxia is the only valid reference condition when assessing the utility of coastal wetlands as fish habitat. Consequently, managers need to investigate the origin of hypoxia, and identify the extent to which it is naturally-driven rather than the consequence of human activities. However, this is no simple task because it can be difficult to identify whether extreme water quality variations in transitional water systems are a response to human-induced stress or if they are natural (Elliott & Quintino 2007).

DO variations are driven by such complex interacting factors, most of which are affected by local vagaries in wetland habitats (i.e. depth, size, connectivity, shading, vegetation cover), therefore it is not practicable to develop meaningful national referential or

international guidelines on the bases of spot measurements, or, even for that matter, by calculating a daily mean or median DO value using multiple spot measurements. To be meaningful, any national guidelines should be supported by high frequency data for a local or regional area in conjunction with exposure risk studies. Too often, exposure risk studies are not supported by field data, or the field data presented include only 1 or 2 days of sampling at one location and therefore do not accurately represent the DO dynamics. Therefore, these studies lose their applicability as they do not represent what fish could be exposed to daily in the environment.

Results obtained from Annandale Wetland can potentially be applied to any similar tropical urbanised wetland found along the GBR coastline. As urban and industrial development expands (Waltham & Sheaves 2015), further degrading water quality (Tsatsaros et al. 2013), strategic environmental assessment need to be conducted to avoid serious consequences that spreading dead-zones would have along the GBR as it is currently seen along the West Coast of the United States (Hogue 2017). A powerful way for environmental managers to identify early warning signs and implement appropriate levels of management intervention (Perna and Burrows, 2005) is to develop accurate models to predict DO, such as D'Autilia et al. (2004) or Peña et al. (2010). This technique, based on high-frequency and long-term water quality measurements, has been recently used in China to provide useful insights for better managing aquaculture ponds (Cui and Chui, 2017). As suggested by Brodie et al. (2008) having a local database, for all priority sites, that is cognisant of high temporal and spatial DO measurements such as those collected during this study, would enhance the predictive ability of models, and assisting with calibration and validation, improve confidence of managers facing the burgeoning challenge of protecting coastal seascapes in a changing world.

2.5. Conclusion

Studying DO is complex and requires caution, especially in tidal and productive ecosystems such as tropical wetlands. DO fluctuated drastically over a 24h cycle in response

to daily PAR, and across the small-scale wetland. Water exchange was also a crucial driver of DO, acting as a natural aerator of the system. This study revealed that fish were exposed almost daily to low DO levels. As this study site represents a typical urbanised tropical wetland found along the GBR coastline, these results suggest similar patterns occur in other coastal wetlands within the region. Continuing urban expansion along the GBR is likely to lead to further coastal water quality degradation. Given the extent of DO fluctuations identified in the present study, further degradation is likely to result in wide-spread development of DO conditions that severely disadvantage species or even exclude them from transitional water systems, particularly in heavily urbanised areas. Therefore, it is important for managers to implement adequate monitoring and develop management strategies to avoid further degradation of these high nursery value habitats. More investigations on local fish exposure risk and fish adaptations to diel-cycling DO, conducted with standardised and realistic methodologies, in conjunction with high frequency DO field data are needed to allow the construction of more accurate models to underpin the development of appropriate management and policies for the sustainable use of coastal wetlands.

2.6. Summary

- In a mangrove wetland, Australia, identified as an important tidal refuge, extreme DO variations were recorded over the tidal and diel cycle, and across a small spatial scale (~10 m). DO was influenced by time of day and tide. Every day, and for around 25% of the logging time, fish were exposed to DO levels that have been linked to increased mortality and reductions in growth, reproduction and activity. These findings emphasised that DO was likely to be an important limiting factor, temporarily reducing the value of this system for fish.

Chapter 3 Patterns of fish utilisation in a tropical Indo-Pacific mangrove-coral seascape, New Caledonia

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3.1. Introduction

Mangrove systems are part of a mosaic of productive coastal habitats (Sheaves, 2005) that provide a variety of services to fish and human populations (Hogarth, 1999; Nagelkerken et al., 2008). Mangrove forests are a fundamental component habitat of mangrove systems (Vance et al., 1996), and confer many of the attributes that make them highly valuable fish habitats (Bell et al., 1984; Beck et al., 2001; Laegdsgaard and Johnson, 2001; Nagelkerken and Faunce, 2007, 2008). However, studies have shown varying degree of mangrove forest utilisation, with for instance a higher contribution of reef fish species to mangrove fish assemblages in the Caribbean compared to several places in the Indo-Pacific (Lal, 1984; Robertson and Duke, 1990; Thollot, 1992; Nagelkerken et al., 2000b; Mumby et al., 2004; Dorenbosch et al., 2005; Dorenbosch et al., 2007; Unsworth et al., 2008; Unsworth et al., 2009; Barnes et al., 2012; Paillon et al., 2014; Sheaves et al., 2016). These observations suggest that not all mangrove forests provide equivalent values to fish. Moreover, recent work in mesotidal Australia suggests that few fish penetrate beyond the forest boundary (Sheaves et al., 2016), suggesting that the use of mangrove forests is spatially heterogeneous. This new evidence raises the question relating to the specific ways in which mangrove forests are utilised by fish. More studies are needed to characterise fish assemblages in mangrove forests with different settings (coastal, estuarine, island, embayment), different tidal ranges (micro-, meso- or macrotidal), proximity of other high value habitats such as seagrass beds and coral reefs, or climatic zones (Sheaves and Johnston, 2008; Unsworth et al., 2008; Igulu et al., 2014; Baker et al., 2015). A better understanding of how mangrove forest utilisation varies

spatially and temporally would provide new insights to help explaining the contrasting results found in the literature.

In many parts of the Indo-Pacific, the tidal range is greater than in the Caribbean, where mangrove forests are usually continually available to fish (Nagelkerken et al., 2008). Intertidal mangrove forests are challenging environments, most notably because they are only available to most aquatic organisms while they are flooded at high tide (Sheaves, 2005; Unsworth et al., 2007; Baker et al., 2015). The intermittent availability of mangrove forests may explain the low use by fish in the Indo-Pacific (Igulu et al., 2014). Indeed, tidal variation (extent, duration and frequency of flooding) generates a range of constraints for fish utilising mangrove forests. Most evident is the decrease in water depth and eventual drainage of the forest as the tide ebbs, forcing fish out of intertidal mangrove forest zones. Several studies have indeed demonstrated that fish undertake regular migrations in tidally driven mangrove systems, with different patterns of mangrove use according to fish species, lunar cycle (neap vs spring tide) and tidal phase (flooding vs ebbing) (Laroche et al., 1997; Krumme, 2004; Ellis and Bell, 2008; Meynecke et al., 2008; Sheaves et al., 2016). Migration of fish in response to tidal movements results in substantial connectivity between the three major tropical coastal habitats: coral reefs, seagrass beds and mangrove forests (Unsworth et al., 2007; Krumme, 2009), giving rise to the idea that mangrove forests are part of a wider interconnected habitat mosaic (Sheaves, 2005). Therefore, investigating tidal and spatial variations in fish assemblages in mangrove forests is a crucial step towards fully appreciating the value and functioning of the whole tropical coastal ecosystem.

The difficulty of sampling these habitats goes a long way towards explaining the paucity of information available on fish assemblages inside mangrove forests (Rozas and Minello, 1997; Unsworth et al., 2009). The use of conventional techniques such as underwater visual censuses or netting techniques is restricted across much of the Australasian region where saltwater crocodiles (*Crocodylus porosus*) are common, and where dense mangrove forests reduce the efficiency of most net-based approaches (Sheaves et al., 2016). Recently, underwater video has been successfully applied to study in-forest fish assemblages (Reis et

al., 2016; Sheaves et al., 2016; Dunbar et al., 2017), most notably because it overcomes a lot of sampling issues, substantially reduces field labour intensity, and allows for high-temporal and -spatial resolution data collection simultaneously in different habitats, such as the edge and the inside of a mangrove forest (Kimball and Able, 2012).

In this study I deployed underwater cameras on the edge and inside a mangrove forest (Ellis and Bell, 2008; Sheaves et al., 2016) coupled with high frequency depth loggers to record spatio-temporal variations in fish assemblages in a microtidal Indo-Pacific mangrove-coral reef seascape. I identified fish species that use the mangrove forest, and used an array of exploratory data analyses and modelling techniques to describe how fish utilisation changes between the forest edge and in-forest habitats, and how fish assemblages vary across the tidal cycle.

3.2. Materials and Methods

3.2.1 Study site

My study focused on a relatively pristine mangrove forest in Bouraké, South Province of New Caledonia (21° 56.971S, 165° 59.481E; Figure 10). New Caledonia is an archipelago located in the South West Pacific, 1,500 km east of Australia. New Caledonia has the largest lagoon in the world, partly registered on the UNESCO World Heritage list. New Caledonia experiences a semi-arid to tropical climate with annual total rainfall of 1,000 mm, and a mixed semi-diurnal microtidal regime (maximum 1.8 m tidal range). Bouraké receives little freshwater inflow with no defined drainage.

The area comprises approximately 2.5 km² of mangrove forest dominated by *Rhizophora stylosa* on the seaward edge and *Avicennia marina* on the landward margin, with a large semi-enclosed central lagoon (1.2 km long, 60 m wide, 1-2 m depth). A channel (20-70 m wide, 2-6 m depth, 700 m long) connects the main lagoon to the coastal waters of Pritzbuer Bay (~ 20 km^2). The channel comprises two sheltered inlets (approximately 0.01 km² each), and a shallow (1-2 m depth) coral reef platform that extends from the middle of the channel to the edge of the mangrove forest. Corals could be seen right on the edge of the

forest in some places. I chose a study location where coral reefs occur in close proximity to mangrove forests (Figure 10), effectively a seascape comparable to the Caribbean coastline (Harborne et al., 2006), so I could relate my findings to this other ecoregion (Spalding et al., 2007) where the tidal range is smaller.

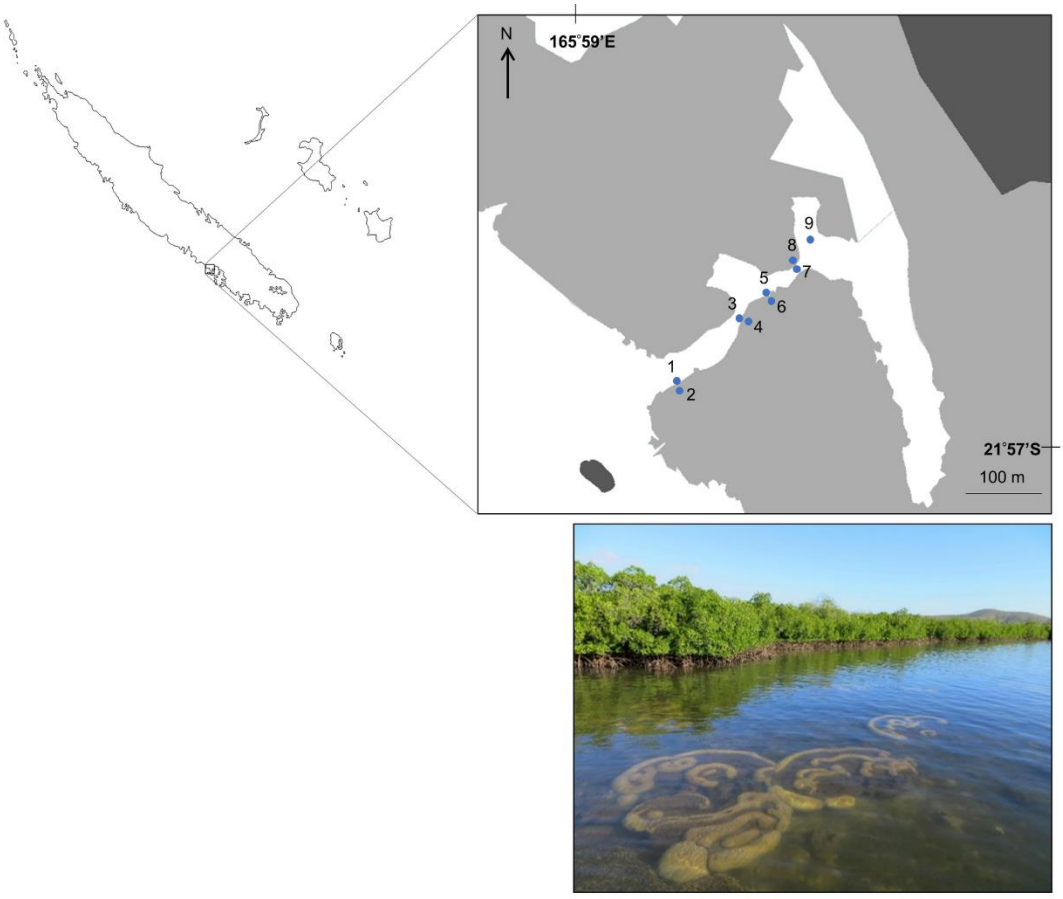

Figure 10 Map and picture of the study system in Bouraké, South Province, New Caledonia. The nine study sites in the mangrove channel sampled from the 21 February to 1 March 2017 are represented by their respective number. Light grey areas represent mangrove forest, dark grey areas represent mainland, and white areas represent water.

3.2.2 Data collection

Fish using the mangrove forest were examined on an inland/offshore gradient along the channel (Figure 10). To assess differences in fish assemblage composition between edge and inside the forest, 4 paired sampling were conducted (sites 1 to 8). Each paired sampling consisted of two sites within 5-7 m distance; the even site number of the paired sampling was located on the mangrove forest edge (defined as the boundary between mangrove prop-roots and bare substrate), and the odd site number located about 5 m inside the forest. Site 9

(considered an edge site in the analyses) was located on the reef platform of the innermost bay, at the edge of scattered mangrove trees slightly away from the main forest. The substrate at sites 1 and 9 consisted of dead corals, small live coral boulders and sand, while on other edge sites it comprised mainly dead corals and small and larger live coral boulders. The substrate was homogeneous and consisted of silt material at in-forest sites.

Fish assemblages were sampled using underwater video cameras (UVCs; Model ATC9K Oregon Scientific) to investigate tidal variations in fish assemblages simultaneously on the edge and inside the forest. Unbaited UVCs mounted on stable bases were deployed at each site during neap (21 to 23 February 2017) and spring tides (28 February to 1 March 2017). A sampling day consisted of cameras first deployed at sites early in the morning (first light), continuing until the battery was discharged, and, with a replacement battery, again deployed mid-afternoon at all sites until the battery was discharged (recording lasted between 2h and 2.5h). Four sampling days were completed (two during neap tides and two during spring tides). Cameras were positioned around 7 cm above the substrate, facing towards the channel. A marker mounted on a flexible rod (3 mm diameter, 0.5 m long) was placed 0.5 m in front of the camera lens as a visibility indicator to ensure a minimum visibility of 0.5 m was achieved in all videos. Visibility was very good and consistent during the sampling period, and fish could be identified confidently up to approximately 2 m from the UVCs in all videos. As depth is one of the main limiting factors to mangrove accessibility, tidal variations in water depth (cm) were measured every 15 minutes at each site with depth loggers (In-Situ Inc. Rugged Troll 100 model). James Cook University issued a permit for a limited impact research to deploy underwater cameras in New Caledonia (no endangered or protected species were involved as no collection of any specimen was conducted). The study area does not benefit from any special protection, therefore, access and activities are not restricted, and no specific permit was required to sample.

3.2.3 Data extraction from videos

While UVCs allow large amounts of data to be gathered quickly in the field, considerable time is required to process these videos. Therefore, I subsampled the acquired video footage. From the two neap tide sampling days, one day was randomly selected and videos at all sites were processed for that day. For the remaining sampling day, all videos were processed from five sites; being the reef platform (site 9) and two pairs of in-forest and forest edge sites (sites 5-8). These sites were selected so one replicate for a site located on the reef platform, and two replicates of paired sites not located on the reef-platform were available. Considering this selection, the sites were then randomly chosen. The same selection was applied to the two sampling days conducted during spring tides.

Once sediments had settled after camera deployment (typically 2-3 min), videos were viewed using VLC media player (VideoLAN, 2001) and subdivided in 5-min intervals to follow tidal variations in fish assemblages. The occurrence of each fish taxon in each 5-min interval was recorded. Only presence/absence data were recorded to avoid biases induced by count data when using UVCs (Sheaves et al., 2016). Fish were identified to the lowest possible taxonomic level. Features useful in discriminating species within some genera or families such as *Plectorhinchus* spp*.,* Mugilidae spp., or Gobiidae spp. were difficult to distinguish in videos, therefore these taxa were identified to genus or family level only. When possible, juvenile fish were identified based on colour patterns and body shape. Any activity such as feeding, hiding, cruising or escaping was also noted. All fish identifications were validated by two additional experts. For each 5-min interval video processed, the information concerning the date of sampling, site, time of day, habitat (edge vs in-forest), lunar phase (neap vs spring), tide direction (flooding vs ebbing), and corresponding water depth was recorded (S1 Appendix).

3.2.4 Data analyses

An index depending on observation per unit effort, similar to the catch per unit effort index (CPUE) when dealing with fishing techniques, was developed to calculate frequencies of occurrence of taxa from the video data. The frequency of occurrence of each taxon was calculated per site (the total number of 5-min intervals in which a taxon was observed at a site

was divided by the total number of 5-min intervals recorded at this site). Only taxa with a frequency of occurrence ≥ 0.05 at one or more sites were retained for analyses (referred to as "common taxa"). Taxa with a frequency of occurrence < 0.05 (referred to as "rare taxa") were excluded from analyses.

Non-metric multidimensional scaling (nMDS) was used as an exploratory analysis to assess differences in fish assemblages among sites during spring and neap tides. The frequency of occurrence of each common taxon was calculated per site per lunar phase. Data were square root transformed (SQRT) to decrease the impact of extreme values, and an nMDS analysis based on Bray-Curtis dissimilarities, the most appropriate distance measure when using abundance data (Bray and Curtis, 1957), was conducted. Clusters within the nMDS were determined by conducting an overlay cluster analysis at 40% and 45% similarity on the dissimilarity matrix of all frequencies of occurrence. A two-way analysis of similarity (ANOSIM) was used to test whether there were significant differences in fish assemblages between sites and lunar phase. Pearson correlations exceeding R > 0.7 between the ordination and taxa were used to fit vectors on the nMDS plot. All analyses were performed using PRIMER 6 software (Clarke and Gorley, 2006). Additionally, frequencies of occurrence of each common taxon at in-forest and edge sites were calculated and plotted using horizontal bar plots to further investigate differences in fish assemblage composition between the two habitats.

To investigate the factors impacting fish presence/absence, a General Linear Mixed Model (GLMM) was conducted using the package "glmm" in R (Knudson et al., 2018). The GLMM was conducted on all the 5-min intervals recorded (S1 Appendix) with presence/absence of any common taxa for each 5-min interval (1 if any common taxa were observed in the 5-min interval, or 0 if no common taxa were observed) as the response variable, "Depth", "Habitat" (edge vs in-forest), "Lunar phase" (neap vs spring), and "Time of day" (morning vs afternoon) as the fixed factors, and "Site", "Date", "Tide direction" (flooding vs ebbing) and a nested effect of "Site" within "Habitat" as the random factors, using a Bernoulli distribution and a logit link function.

Cumulative depth frequency curves were plotted for each site to highlight differences in temporal dynamics. To further understand how fish utilisation varies across depth, variations of SQRT frequencies of occurrence across depth, over flooding and ebbing tide on the edge and in-forest were assessed using a General Additive Mixed Model (GAMM). Each 5-min interval was allocated to a class of water depth of 10 cm (from 10-20 cm to 120-130 cm) according to the water depth value recorded, and the SQRT frequencies of occurrence of each common taxon was calculated per class of water depth during flooding and ebbing tide per habitat (the total number of 5-min intervals in which a taxon was observed at a class of depth during flooding and ebbing tide per habitat was divided by the total number of 5-min intervals recorded for this same sample unit). Frequencies of occurrence were SQRT to reduce the impact of extreme values. To avoid false absence recordings, taxa never recorded in the habitat of interest were not considered (i.e. if a taxon was never recorded in-forest during the study it was not included in the in-forest analysis). To run the GAMM, SQRT frequencies of occurrence were used as the response variable, “Depth” as a smooth term, and “Habitat” and “Tide direction” as parametric terms using a Gaussian distribution and an identity link function. “Habitat” was included in the model to avoid any nesting issue. The model was built using the package “mgcv” in R (Wood, 2007). Patterns of variations of SQRT frequencies of occurrence were then investigated graphically using boxplots to examine the variations of average SQRT frequencies of occurrence among taxa at each depth interval, and a LOESS curve was fitted to the data to analyse the general pattern of habitat use. Patterns of mangrove habitat use for each taxon were then plotted using a LOESS curve and individually assessed graphically to examine similarities and classify patterns of fish occurrence across depth. Taxa were grouped in similar patterns if their maximum average occurrence was observed at a similar depth stage. Three equivalent depth stages were defined for this purpose: Low depth (between 10-20 and 40-50 cm); Intermediate depth (between 50-60 and 80-90 cm); High depth (between 90-100 and 120-130 cm).

3.3. Results

3.3.1 Fish composition

Fifty-six video deployments were analysed (totalling more than 118h of video). Seventy-two taxa from 29 families were recorded, with 36 common taxa (frequency of occurrence ≥ 0.05 on at least one site) retained for further statistical analyses (Table 3). Most species recorded were marine and reef-associated (Froese and Pauly, 2017) including fish of families Scaridae, Chaetodontidae, Pomacanthidae, Siganidae, Acanthuridae, Lutjanidae, or Labridae.

Table 3 Summary of all the families and taxa identified at Bouraké, New Caledonia.

Family	Taxon
Acanthuridae	***Acanthurus auranticavus**** [1]
	Acanthurus grammoptilus [2]
	Acanthurus sp. cf *blochii*
	Ctenochaetus sp.
	Zebrasoma velifer
Apogonidae	***Fibramia lateralis**** [3]
	Ostorhinchus septemstriatus
Belonidae	*Belonidae* spp.
Blenniidae	*Blenniidae* spp.
Carangidae	*Caranx ignobilis*
	Caranx papuensis [1]
	Caranx sp.
Chaetodontidae	***Chaetodon auriga**** [2]
	Chaetodon bennetti [2]
	Chaetodon ephippium
	Chaetodon flavirostris
	Chaetodon lineolatus [2]
	Chaetodon lunula [2]
	Chaetodon melannotus
	Chaetodon speculum
	Chaetodon vagabundus [2]
	Heniochus acuminatus [1]
Clupeidae	**Clupeidae spp.** [2]
Diodontidae	*Diodon hystrix*
Ephippidae	*Platax pinnatus*
Fistulariidae	*Fistularia* spp.
Gerreidae	*Gerres filamentosus*
	Gerres oyena* [4]
Gobiidae	*Amblygobius linki*
	Amblygobius nocturnus
	Amoya gracilis [3]
	Asterropteryx* sp. cf *striata [4]

Table 3 (continued)

Family	Taxon
Haemulidae	*Plectorhinchus lineatus*
	***Plectorhinchus* spp.** [2]
	Pomadasys argenteus [2]
Hemiramphidae	*Hyporhamphus* sp.
Labridae	*Choerodon graphicus*
	Labridae spp.
Lethrinidae	***Lethrinus harak**** [2]
	Lethrinus lentjan [1]
	Lethrinus obsoletus
Lutjanidae	***Lutjanus argentimaculatus**** [3]
	Lutjanus fulviflamma [4]
	Lutjanus fulvus [1]
	Lutjanus russellii [2]
Monodactylidae	***Monodactylus argenteus**** [1]
Mugilidae	**Mugilidae spp.*** [3]
Mullidae	***Mulloidichthys flavolineatus*** [2]
	Parupeneus ciliatus
	Parupeneus indicus [4]
	Upeneus tragula [1]
Pomacanthidae	***Pomacanthus sexstriatus*** [2]
Pomacentridae	***Neopomacentrus* spp.** [2]
Scaridae	*Bolbometopon muricatum*
	Scarus* sp. cf *ghobban [1]
Scatophagidae	*Scatophagus argus*
Serranidae	*Epinephelus caeruleopunctatus*
	Epinephelus lanceolatus
	Epinephelus malabaricus
	Epinephelus sp.
Siganidae	***Siganus canaliculatus*** [1]
	Siganus lineatus* [2]
	Siganus punctatus

Cryptocentrus leptocephalus [2]	Sparidae	***Acanthopagrus* sp. cf *akazakii*** [2]
Eviota sp.	Sphyraenidae	*Sphyraena barracuda*
Exyrias puntang	Tetraodontidae	*Arothron hispidus*
Gobiidae spp.* [3]		
Gobiidae spp.2		
Redigobius balteatus [3]		

*Taxa highlighted in bold represent the common taxa (frequency of occurrence ≥ 0.05 on at least one site) that were kept for statistical analyses. Taxa highlighted with a * represent the 10 most common taxa. Taxa or families underlined mean that juveniles were potentially observed for that taxon or for at least one taxon within the family that could not be identified. The superscript number corresponds to the pattern of mangrove habitat utilisation across depth followed by the taxon as described in Figure 15: 1) High-depth users; 2) Intermediate-depth users; 3) Low-depth users; 4) Generalist users.*

Fish composition varied significantly among sites (ANOSIM: R = 0.793, p < 0.001), with distinct assemblages generating three and four different clusters at 40 % and 45 % similarity respectively on the nMDS plot (Figure 11). At 40 % similarity, the 1st cluster comprised all the samples conducted in-forest. The samples were characterised by a lower taxonomic richness (23 common taxa; Figure 12) dominated by *Fibramia lateralis* and all the taxa belonging to the Gobiidae family (except *Cryptocentrus leptocephalus* and *Asterropteryx* spp.), that were the only taxa recorded almost exclusively at in-forest sites (Figure 12). The 2nd cluster comprised all the samples conducted on the edge but site 7 at spring tide. The samples were characterised by a higher taxonomic richness (34 common taxa; Figure 12), among which 10 taxa, mostly reef-associated, significantly contributed to the fish assemblage composition at edge sites (Figure 11). Site 7 at spring tide was an outlier and made the 3rd cluster driven by the abnormally high occurrence of *Neopomacentrus* spp. (Figure 11). Interestingly at 45 % similarity, another cluster was generated, separating deep edge and shallow edge sites (Figure 12; Figure 13). Three species of snappers, *Lutjanus fulviflamma, Lutjanus argentimaculatus and Lutjanus russellii* were the only three species not showing apparent preference for edge or in-forest sites as they were almost evenly recorded on the two habitats (Figure 12), and therefore did not significantly characterised any of the two habitats (Figure 11). Replicate samples plotted close to each other and were grouped in the same clusters (Figure 11). Lunar phase did not significantly influence fish assemblages (ANOSIM: R = 0.2, p > 0.2).

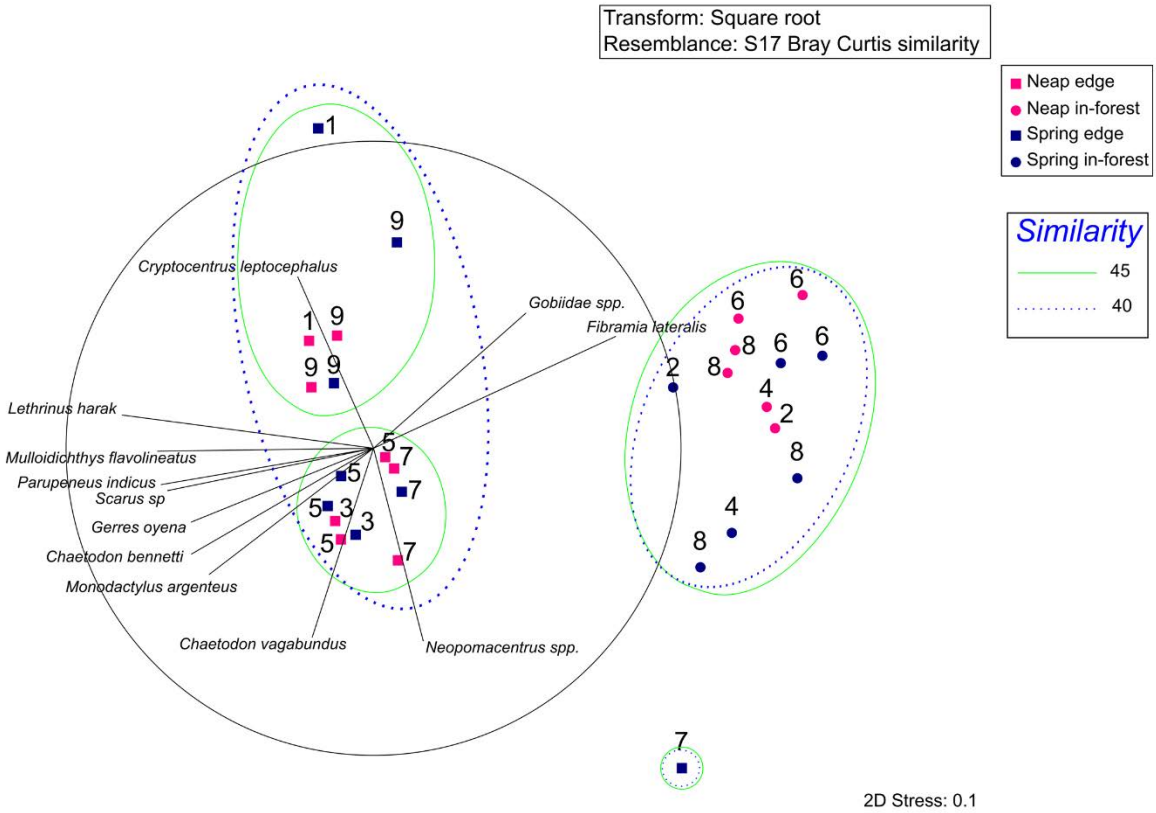

Figure 11 nMDS analysis performed on square root transformed frequencies of occurrence for each taxon per site per tide.
Edge sites are represented by squares and in-forest sites by circles. Sites sampled at neap tide are coloured in deep pink, and sites sampled at spring tide in navy blue. Solid green and dotted blue ellipses represent overlay clusters determined at 45 and 40 % similarity respectively. Vectors represent taxa with a Pearson correlation with the ordination R > 0.7.

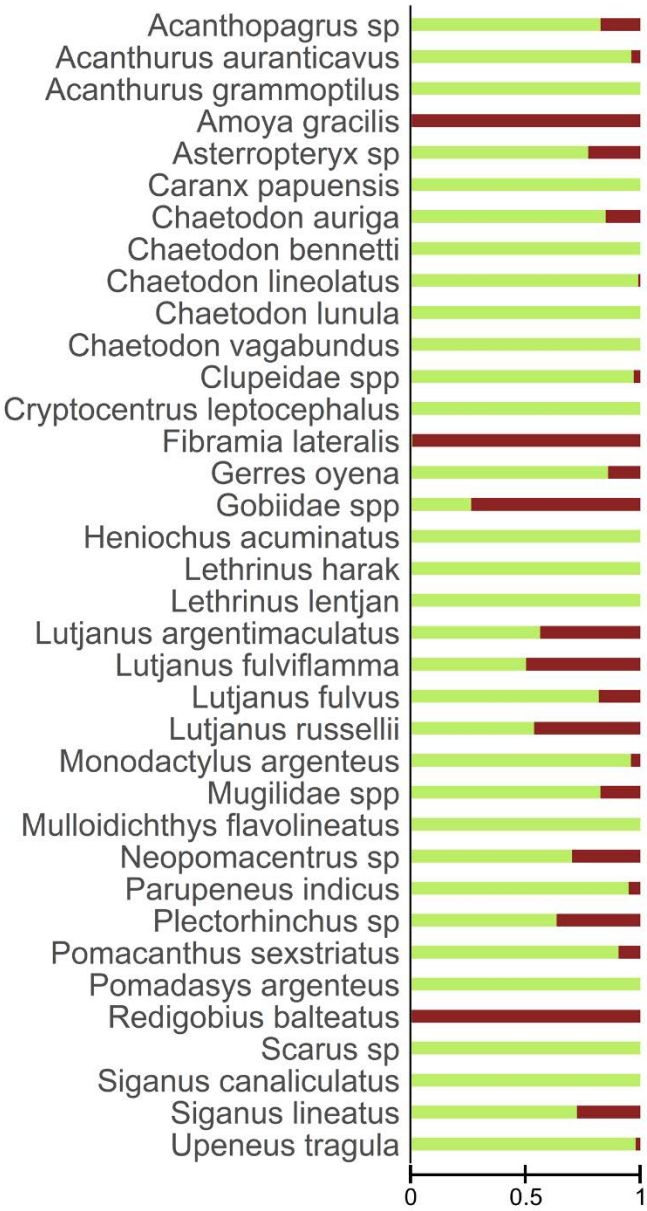

Figure 12 Proportion of time spent by each of the common taxa on the edge versus inside the forest. edge=green and in-forest=brown. Proportions range from 0 to 1, 1 corresponding to a taxon exclusively recorded on the edge or in-forest and 0.5 corresponding to a taxon recorded on the edge as frequently as in-forest.

"Habitat" (GLMM: $z = -2.637$; $p < 0.005$), "Lunar phase" (GLMM: $z = -9.406$; $p < 0.001$) and "Depth" (GLMM: $z = -2.118$; $p < 0.05$) significantly influenced the presence/absence of taxa. However, "Time of day" (GLMM: $z = -1.519$; $p > 0.1$), date of sampling (GLMM: $z = 1.555$; $p > 0.05$), "Tide direction" (GLMM: $z = 0.991$; $p > 0.1$) and sites within a same habitat (GLMM: $z = 1.394$; $p > 0.05$) did not significantly influence presence/absence of taxa. Further data exploration following the GLMM results showed that at edge sites there was a higher proportion of 5-min intervals in which a taxon was observed compare to in-forest sites.

Similarly, during neap tides, there was a higher proportion of 5-min intervals in which a taxon was observed compare to spring tides (S2 Appendix).

3.3.2 Tidal variations in fish assemblages

Average depth was substantially shallower at in-forest than edge sites (neap tides (mean ± SE): 34 ± 0.57 and 55 ± 0.66 cm respectively; spring tides: 48 ± 1.11 and 71 ± 1.23 cm respectively), as was maximum depth (95 cm and 133 cm respectively; Figure 13). Moreover, in-forest sites were exposed (i.e. not flooded) for 4-5 h per day during neap tides, and 2-3 h per day during spring tides, while sites on the edge were always submerged. Sites could be classified into three groups according to depth profiles (Figure 13): deep edge sites (sites 3, 5, 7; maximum depth 133 cm); shallow edge sites (sites 1 and 9; maximum depth: 107 cm); in-forest sites (sites 2, 4, 6, 8; maximum depth: 95 cm; Figure 13).

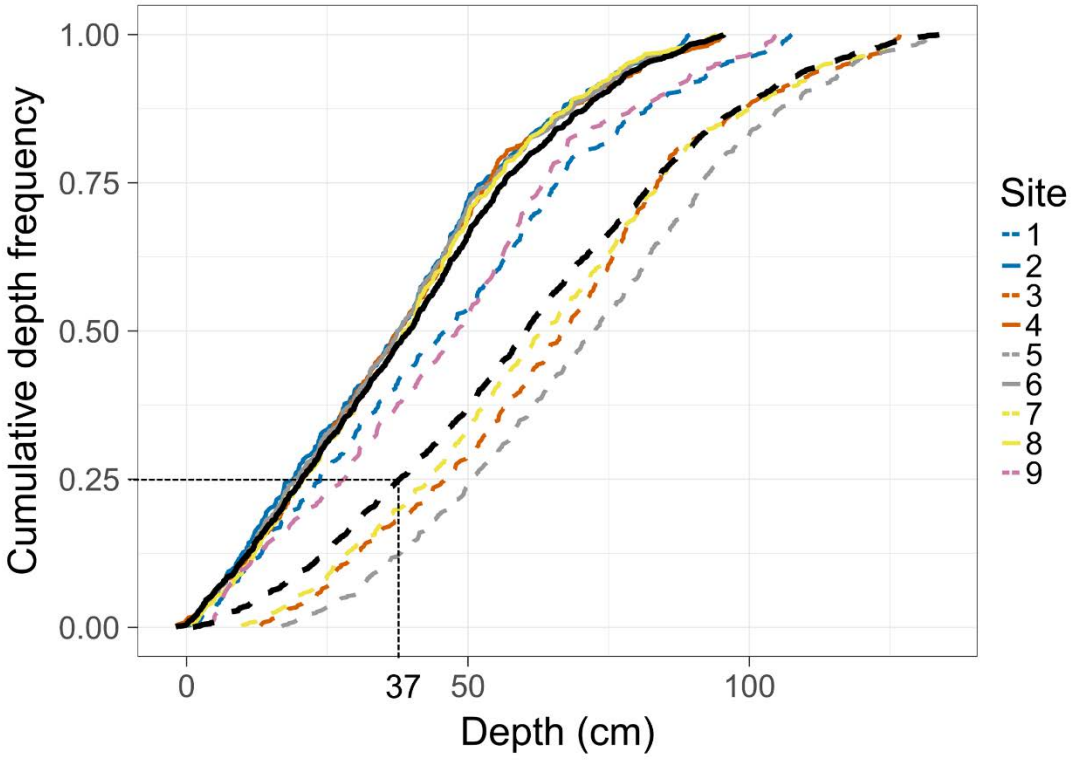

Figure 13 Site-specific cumulative depth frequencies.
Each colour represents a paired edge and in-forest site, and edge sites are represented by dashed lines and in-forest sites by solid lines. The dashed dark line indicates the mean cumulative depth frequencies across all edge sites. The solid black line indicates the mean cumulative depth frequencies across all in-forest sites. An example is provided to help interpret the figure (for 25 % of the recorded time depth was on average equal or below 37 cm at edge sites).

As the GLMM showed that depth had a significant effect on presence/absence of taxa, a GAMM was used to further explore the response of frequencies of occurrence of fish across increasing and decreasing depth (equivalent to flooding and ebbing tide) and by habitat. SQRT frequencies of occurrence of fish significantly varied across depth (GAMM: $F = 6.756$; $p < 0.001$; S3 Appendix), and significantly differed between “Habitat” (GAMM: $F = 39.792$; $p < 0.001$) and “Tide direction” (GAMM: $F = 9.056$; $p < 0.005$). Magnitude of variations in SQRT frequencies of occurrence across depth was higher at edge than in-forest sites (Figure 14, S3 Appendix). However, the patterns were similar between the two habitats, with overall frequencies of occurrence highest at intermediate depth values, especially at ebbing tide, and lowest at extreme depth values (low or high depth; Figure 14, S3 Appendix).

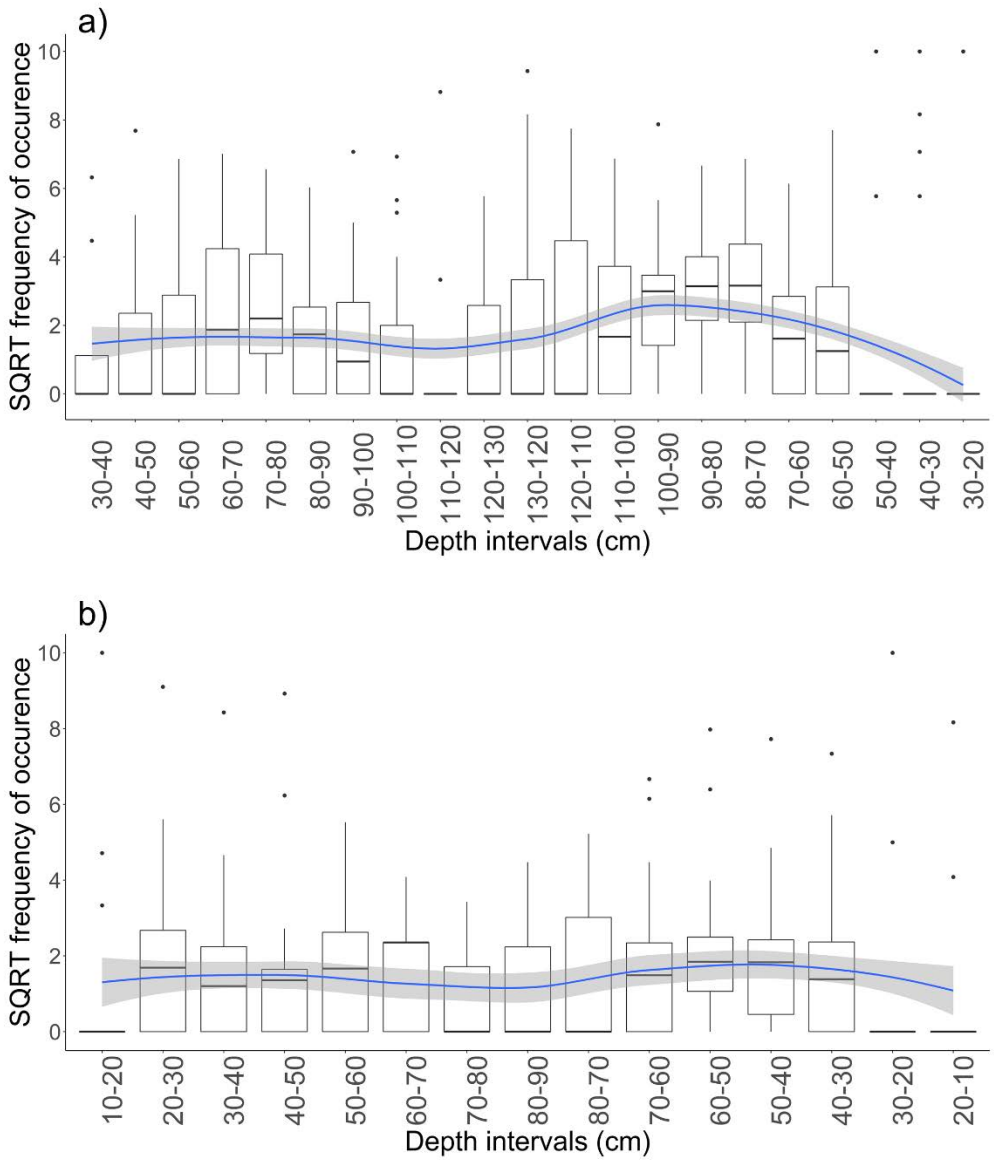

Figure 14 Boxplots of average square root transformed frequency of occurrence of common taxa across depth on a) edge sites; b) in-forest sites.
The blue line is the LOESS curve representing the general pattern of habitat use for all common taxa considered. Shaded area around the LOESS curve represents the 95% confidence interval. On Figure 14b, interval 90-80 cm has been removed as no data were recorded.

Similarities in mangrove forest utilisation among common taxa clearly determined 4 main patterns of utilisation: 1) taxa with higher frequencies of occurrence at highest depth values (90-130 cm; High-depth users); 2) taxa with higher frequencies of occurrence at intermediate depth values (50-90 cm; Intermediate-depth users); 3) taxa with higher frequencies at low depth values (10-50 cm; Low-depth users); 4) taxa with similar frequencies of occurrence across depth (Generalist users); Figure 15, S4 Appendix).

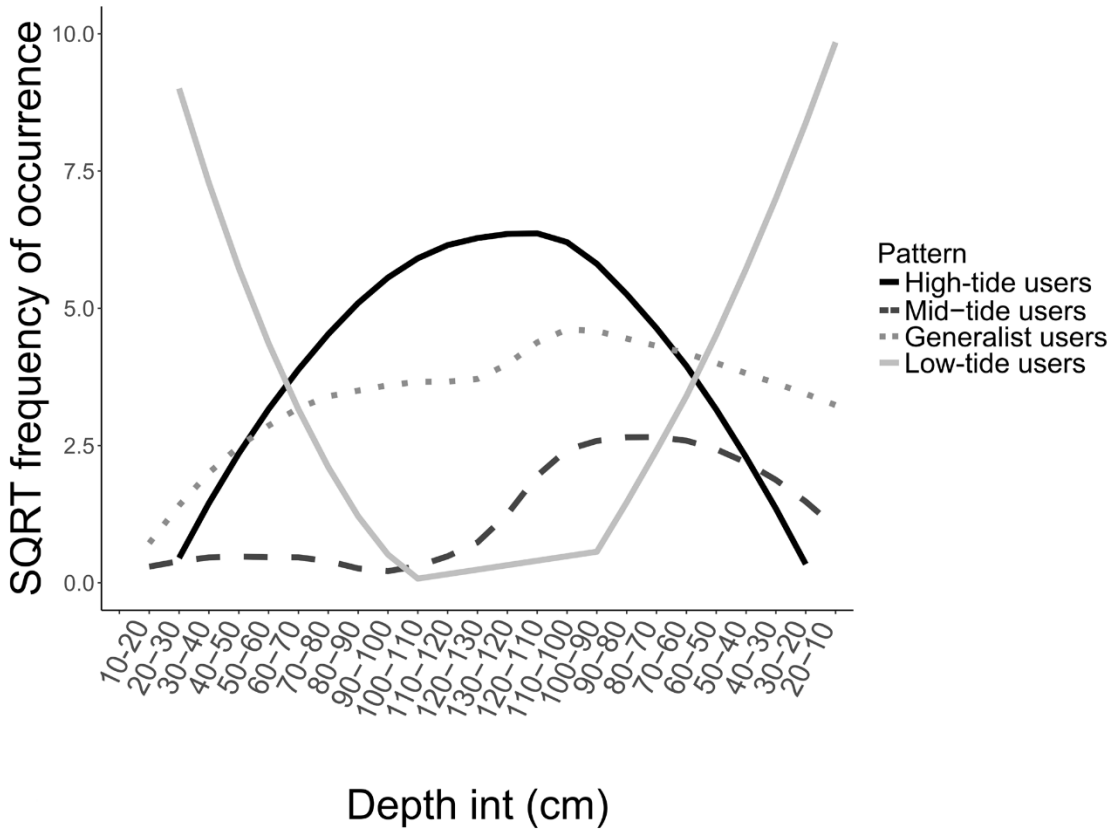

Figure 15 Patterns of mangrove habitat utilisation across the depth profile.
The curves represent the LOESS curves constructed with the square root transformed frequencies of occurrence of fish across depth. Common taxa followed four main patterns of mangrove habitat utilisation across depth: 1) taxa using mangrove habitats mainly at high depth values (High-depth users); 2) taxa using mangrove habitats mainly at intermediate depth values (Intermediate-depth users); 3) taxa using mangrove habitats mainly at low depth values (Low-depth users); 4) taxa without any apparent preferences for depth (Generalist users). Table 3 identifies the taxa allocated to each category.

3.4. Discussion

Understanding the spatial and temporal variations in the use of mangrove habitats by fish is important when considering conservation and resource management to protect mangrove ecosystems from human and natural disturbances. This study highlights that the edge and inside of mangrove forests, the two major component habitats of mangrove forests, featured distinct taxonomic diversity and fish assemblage composition. Fish assemblages varied significantly across the tidal cycle, with species-specific patterns of mangrove habitat utilisation. Spatial differences in water depth among sites within a same habitat also seemed to influence fish assemblages across this mangrove/coral system. While only a small portion

of the species observed on nearby coral reefs were recorded in Bourake, I found that this mangrove forest does have a role in supporting reef fish species, emphasising the importance of Indo-Pacific mangroves as valuable fish habitats.

The setting of this tropical mangrove/coral system influenced the nature of the fish assemblages recorded. At least 72 taxa made use of this relatively small mangrove/coral system, with most species classified as tropical marine and reef-associated (Froese and Pauly, 2017). Most taxa recorded have not been identified as mangrove-associated in previous studies in coastal mangroves in the west Pacific (Robertson and Duke, 1990; Sheaves et al., 2007b; Sheaves et al., 2016), suggesting that their presence is linked to the proximity of coral reefs, further supporting the contention that mangrove-coral habitats are interconnected. Conversely, many fish families important in other Indo-Pacific mangrove systems remote from coral reefs, such as Leiognatidae, Ambassidae, Sillaginidae, Terapontidae, or Toxotidae (Thollot, 1989; Robertson and Duke, 1990; Laroche et al., 1997; Sheaves et al., 2016) were not recorded in Bouraké. Most individuals observed were at a sub-adult stage, however, juveniles where occasionally recorded for several taxa. Juveniles of at least 12 reef fish species were commonly recorded (*Lutjanus fulviflamma*, *Lutjanus argentimaculatus, Lutjanus russellii*, *Lethrinus* spp. (2 species), *Bolbometopon muriculatum*, *Siganus lineatus*, *Caranx* sp., *Epinephelus caeruleopunctatus*, *Scarus* sp., *Acanthurus* sp., *Neopomacentrus* sp.). Additionally, relatively small individuals of *Epinephelus lanceolatus* and *Acanthopagrus akazakii* were observed. Thus, the fish community using this system consisted of a substantial number of juvenile reef species, including juveniles of two species classified as vulnerable on the IUCN list (*E. lanceolatus* and *B. muricatum*), and one endemic species (*A. akazakii*) (Iwatsuki et al., 2006). These findings highlight that near-coral mangrove habitats in the Central Indo-Pacific, such as Bouraké, have a role in providing habitats for juvenile reef fish in parallel to the situation in the Tropical Atlantic (Sedberry and Carter, 1993; Nagelkerken et al., 2002; Mumby et al., 2004).

While early studies concluded that high connectivity between coral reefs and mangroves had little influence on mangrove fish assemblages (Quinn and Kojis, 1985; Thollot,

1992; Laroche et al., 1997), recent evidence suggest that in many instances there is a high occurrence of reef-associated fish in mangroves adjacent to reefs (Dorenbosch et al., 2007; Unsworth et al., 2009; Barnes et al., 2012; Olds et al., 2013). While supporting this idea, the current study emphasises that the utilisation and value of mangrove forests vary locally and cannot be generalised from one system to another (Dorenbosch et al., 2007; Unsworth et al., 2008; Sheaves et al., 2016).

This study highlighted clear spatial variations in fish assemblages across the two different habitats mangrove edge and mangrove in-forest. Indeed, fish assemblages were distinctly different between the mangrove edge and just a few meters inside the mangrove forest. Most fish were recorded cruising on the edge of the mangrove forest, while sightings inside the mangrove forest were sparser. Two main hypotheses, namely increased food supply and providing shelter, have been suggested to explain why fish use mangrove forests. However, neither of these two hypotheses were confirmed by the current study as few foraging activities were recorded and few individuals were observed actively sheltering among mangrove prop-roots. In fact, few species made regular use of the mangrove forest, supporting the idea that most fish species simply remain on the edge and potentially retreat into the forest for opportunistic feeding, or to escape presence of larger predators (Laegdsgaard and Johnson, 2001). This result aligns with the observations in estuarine mangrove forests of northern Australia where few species made regular use of the in-forest habitat (Sheaves et al., 2016). These two habitats (edge and in-forest) probably confer different values to fish, however, fish could benefit from most attributes that physically attract them in mangrove systems (Nagelkerken and Faunce, 2008) by using the mangrove fringe without venturing into the forest. This result supports the idea that high tidal range leading to forest drainage limits the use of mangrove forests in the Indo-Pacific compare to the Caribbean. Accessing the forest could be disadvantageous because of increased risk of becoming trapped after the tide falls, but could also be linked to adverse water quality such as low dissolved oxygen that develops at low tide (Chapter 2; Mattone and Sheaves, 2017).

Fish assemblages exhibited small-scale spatial (dozens of meters) heterogeneity, particularly along the forest edge compared to in-forest sites. There was a clear distinction in terms of fish assemblages in the nMDS plot between sites 1 and 9, and sites 3, 5 and 7. This pattern could be explained by water depth profile and substrate differences, with sites 1 and 9 featuring dead corals, small live coral boulders and sand, and shallow depth, while other edge sites also had dead corals, along with small and larger live coral boulders but lacked sand, and experienced deeper depth. Conversely, all the in-forest sites were quite similar in terms of fish assemblages, suggesting that they provide a homogeneous habitat with similar substrate and depth profile throughout the system. Johnston and Sheaves (2007) also identified species-specific responses to different small-scale habitats according to their depth and substrate composition. The importance of accounting for spatial heterogeneity of fish assemblages when characterising the habitat value of a system, or when using fish assemblages as a bio-indicator of ecological change or ecosystem health (Whitfield and Elliott, 2002), was highlighted by Becker et al. (2012) who observed the influence of small spatial scale changes in water depth and substrate composition on fish assemblages at seagrass beds in South Africa.

Fish assemblages varied temporally across the tidal cycle. Tide-induced depth variations have been linked to changes in fish assemblages (Laroche et al., 1997; Ellis and Bell, 2008; Becker et al., 2012; Harborne et al., 2016). This result was corroborated here as fish assemblages varied across depth, with more fish observed during intermediate depth values, especially at ebbing tides, and most species generally avoiding extreme shallow or deep water. In fact, fish displayed species-specific responses to depth with four main patterns identified: 1) taxa using mangrove habitats mainly at high depth values (High-depth users); 2) taxa using mangrove habitats mainly at intermediate depth values (Intermediate-depth users); 3) taxa using mangrove habitats mainly at low depth (Low-depth users); 4) taxa without any apparent preferences for depth (Generalist users). Patterns 3 and 4 mainly comprised taxa that frequently used mangrove habitats such as *Fibramia lateralis*, *Lutjanus argentimaculatus*, *Siganus lineatus*, *Gerres oyena*, or taxa belonging to the Gobiidae family (Sheaves et al.,

2016), while the other two profiles comprised mainly marine and reef-associated species. In essence, rather than accessing mangrove habitats as soon as they become available, many species seem to use mangrove habitats only for a restricted period of time. Other studies that looked at variations in fish assemblages across the tidal cycle also reported species-specific responses to the depth profile and highlighted that species using mangrove habitats extensively were accessing them at a shallower depth than other less frequently observed species (Bretsch and Allen, 2006; Ellis and Bell, 2008; Castellanos-Galindo et al., 2010; Becker et al., 2012; Harborne et al., 2016; Reis-Filho et al., 2016). Factors driving these tidal migrations are not fully understood, and the fact that species do not enter mangrove habitats as soon as they become available may suggest that these patterns could be the result of behavioural adaptations to avoid adverse water conditions such as low dissolved oxygen that can occur early or late in the tide (Chapter 2; Mattone and Sheaves, 2017). Species using extensively mangrove habitats could be adapted to tolerate lower depth and adverse dissolved oxygen conditions compare to species that would occasionally use mangrove habitats when they are more suitable. More studies are needed to link tidal fish migrations with dissolved oxygen conditions in mangrove habitats because dissolved oxygen is likely to be a critical environmental factor determining the value of these habitats.

Lunar phase was another influential factor responsible for temporal variations in mangrove habitats utilisation by fish. More fish were detected during neap tide than spring tide, however, taxonomic richness and fish assemblage composition were similar. These data oppose previous studies that observed more fish at spring tide than neap tide (Hampel et al., 2003; Krumme et al., 2004; Ramos et al., 2011). These authors suggest that spring tides result in more habitats available and for longer duration, attracting more fish. I firstly thought this was an artefact of the methodology, with fish disappearing from the field of view as water became too deep. However, I compared fish occurrence within the same depth intervals between neap and spring tides, and fish presence was still substantially lower during spring tides, which suggests that there may be another explanation. One explanation could be that at spring tides fish can access more intertidal habitats, reducing the probability of encounter with the UVCs.

I also observed very strong currents in the channel and along the mangrove edge during spring tides that could reduce the time fish can benefit from using mangrove habitats as the energy needed to remain on the mangrove edge may be too high.

3.5. Conclusion

The results here provide further support that within a mangrove forest, the inside and edge of the forest are two distinct habitats characterised by different fish assemblages. The study mangrove forest plays a role in maintaining a substantial number of fish species. However, the habitats use was species-specific, suggesting that utilisation and value need to be considered species-by-species if we want to fully understand the role mangrove systems play in maintaining fish communities. The high spatial and temporal heterogeneity of fish assemblages complicates the characterisation of mangrove forests value and utilisation, suggesting that results from one location are unlikely to be applicable to other systems more broadly. This is an important conclusion for managers when considering to adapt conservation strategies from other locations, to local-specific habitat mosaics.

3.6. Summary

A mangrove forest in New Caledonia was studied to determine how fish responded to tidal fluctuations, potentially reducing the habitat quality. Fish assemblages were very distinct between the mangrove edge and 5 m inside the forest (in-forest), with few taxa making extensive use of the in-forest habitat. These results highlight that the different components of mangrove forests probably confer different values to fish, and showed that for most taxa, using the in-forest habitat may not be beneficial. The species-specific patterns of mangrove habitats utilisation observed over tidal scales indicated that fish were responding to one or several factors covarying with tide.

Chapter 4 Hypoxia in mangroves: occurrence and impact on valuable tropical fish habitat

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4.1. Introduction

Mangrove forests are recognised as important habitats for fish (Robertson and Duke, 1990; Nagelkerken et al., 2002; Nagelkerken et al., 2008). However, their value has been shown to be heterogenous and influenced by local environmental factors influencing mangrove forests accessibility and suitability (Faunce and Serafy, 2006; Bradley et al., 2019). Mangroves can be challenging habitats, especially in regions where they are subjected to tide (Unsworth et al., 2007; Olds et al., 2012), as tidal variation generates a range of constraints for marine organisms. Indeed, mangrove forests generally become only accessible for short periods while flooded at high tide, and the decrease in water depth as the tide ebbs leads to eventual drainage of the forest (Sheaves, 2005; Baker et al., 2015). Tidal variation also induces short-term changes in environmental conditions such as salinity, temperature, water depth, turbidity, light, and dissolved oxygen (DO), that can lead to a temporarily unsuitable habitat for fish utilisation (Chapter 2; Davis, 1988; Rountree and Able, 2007; Brady and Targett, 2013; Mattone and Sheaves, 2017).

Several studies have demonstrated that fish undertake regular migrations in intertidal mangrove forests. Migration patterns have been shown to be species-specific and influenced by tide (Chapter 3; Laroche et al., 1997; Krumme, 2004; Ellis and Bell, 2008; Meynecke et al., 2008; Sheaves et al., 2016). Tidal migrations indicate that fish respond to one or several factors varying with tide. However, there is still uncertainty on what environmental factors induce these tidal migrations. The factors driving these species-specific tidal migrations could

be changing water depth (Bretsch and Allen, 2006; Ellis and Bell, 2008; Reis-Filho et al., 2016), or alternatively the result of active avoidance to adverse changes in water quality.

A key factor determining water quality and that can rapidly fluctuate across tide is DO. DO is crucial for all aerobic organisms, including fish (Driedzic and Hochachka, 1978; Falkowski and Raven, 1997). However, DO availability varies extremely over the tidal- and diel-cycle in mangrove habitats, reaching levels that can lead to physiological stress (Chapter 2; Knight et al., 2013; Gedan et al., 2017; Mattone and Sheaves, 2017). Consequently, it is likely that some fish species respond to changes in DO by undertaking tidal migrations, or by avoiding mangrove forests permanently to prevent the adverse effects following exposure to low DO. Despite the importance of DO and its extreme variability in shallow-water environments, our understanding on how DO fluctuations shape patterns of fish utilisation on a tidal and diel scale is limited (Davis, 1988; Smith and Able, 2003; Rountree and Able, 2007).

DO is maybe the most complex and variable parameter to study, as it is influenced by multiple interacting biotic and abiotic parameters at a range of spatial and temporal scales (Buffoni and Cappelletti, 1999; Diaz and Rosenberg, 2008; Nezlin et al., 2009). However, minimum and maximum DO levels are partially predictable, with the lowest DO levels occurring at night or dawn at low tide, following nighttime respiration, while maximum levels are recorded in the afternoon at high tide, following autotrophic production (Kenney et al., 1988; Mazda et al., 1990; D'Avanzo and Kremer, 1994; Tyler et al., 2009). This diel pattern gives part of the answer of when fish could use mangrove habitats without being exposed to high risks of low DO. However, fish species have developed physiological and behavioural adaptation strategies (Kramer, 1987; Breitburg, 1994; Diaz and Rosenberg, 1995), leading to species-specific hypoxia tolerances (Vaquer-Sunyer and Duarte, 2008). Consequently, these adaptations could result in species-specific tidal migrations of nekton, as species highly tolerant to hypoxia would be adapted to use more often and remain longer in mangrove forests, compared to other less tolerant species that would be restricted to access mangrove forests at higher DO levels.

Although it is known that other mangrove forests in the Indo-Pacific experience natural low DO (Knight et al., 2013; Mattone and Sheaves, 2017), it is unknown how general this phenomenon is, and what are the potential consequences on fish populations. Understanding DO dynamics and the impacts on fish utilisation and value of highly productive habitats such as mangroves is crucial, especially in the context of global ocean deoxygenation (Diaz and Rosenberg, 2008; Breitburg et al., 2018). Ocean deoxygenation is mainly due to the increase of human activities along the coastlines during the past 50 years responsible for the release of nutrient-enriched effluents (Vaquer-Sunyer and Duarte, 2008), implying that mangrove forests are especially vulnerable to anthropogenic deoxygenation due to their location along the coasts. By addressing the gaps of knowledge around hypoxia in mangrove forests, managers would be in a stronger position to implement adequate action plans to limit the impact of hypoxia that is predicted to worsen in the coming years (Breitburg et al., 2018).

This study examines the impact of DO fluctuations on the utilisation of mangrove forests by fish in a mangrove-coral reef seascape in the Indo West Pacific (IWP). I assessed how fish utilisation changes across tidally varying DO levels, and I determined the relative importance of DO, depth, lunar phase (neap vs spring), location within the mangrove forest (edge vs in-forest), time of day, and tide direction (flooding vs ebbing) in explaining variations in fish assemblages. To address this aim, I used unbaited underwater video cameras, simultaneously deployed at dawn and mid-afternoon on the edge and 5 m inside a mangrove forest, coupled with high frequency DO and depth loggers. The study site was located in an IWP mangrove-coral reef seascape experiencing a microtidal regime.

4.2. Materials and Methods

4.2.1 Study site

The study was conducted in a semi-enclosed lagoon (1.2 km long, 60 m wide, 1-2 m depth) located in Bourake, South Province of New Caledonia (21° 56.971S, 165° 59.481E; Figure 10). The system comprises a 2.5 km^2 mangrove forest dominated by *Rhizophora stylosa* on the seaward edge and *Avicennia marina* on the landward margin. A channel (20-

70 m wide, 2-6 m depth, 700 m long) bisects the mangrove forest and connects the semi-enclosed lagoon to the coastal waters of Pritzbuer Bay (~ 20 km^2). The channel comprises two sheltered inlets (approximately 0.01 km^2 each), and a shallow (1-2 m depth) coral reef platform that extends from the middle of the channel to the edge of the mangrove forest. New Caledonia is an archipelago located in the South West Pacific, around 1500 km east of Australia. It is characterised by a semi-arid to tropical climate with annual total rainfall of 1000 mm, and a mixed semi-diurnal microtidal regime (maximum 1.8 m tidal range). The study system receives little freshwater inflow with no defined drainages.

4.2.2 Data collection

Nine sites were selected on an inland/offshore gradient along the channel (Figure 10). Sites 1 to 8 were 4 paired sites, with odd site numbers located on the mangrove forest edge (defined as the boundary between mangrove prop-roots and bare substrate) and even site numbers located 5 m inside the mangrove forest. Site 9 was located on the edge of scattered mangrove trees growing on the reef platform of the innermost inlet and was considered as an edge site.

Fish assemblages were examined at the sites using unbaited underwater video cameras (UVCs). UVCs were deployed at dawn until the battery was discharged (around 2.5 h) and again mid-afternoon, during neap (21 to 23 February 2017) and spring tides (28 February to 1 March 2017), simultaneously at the 9 sites. This sampling design was applied to capture fish assemblages as close as possible to the expected lowest daily DO levels (dawn), and the expected highest DO levels (mid-afternoon; Chapter 2). Cameras were positioned around 7 cm above the substrate, facing towards the channel. A marker was placed 0.5 m in front of the camera lens as a visibility indicator to ensure all videos had a minimum visibility of 0.5 m. Visibility was relatively consistent during the sampling period, and fish could be identified confidently up to approximately 2 m from the UVCs in all videos.

Over this study, I examined the effects of: tidal factors (depth, lunar phase (spring vs neap) and tide direction (flooding vs ebbing)) related to habitat accessibility; DO, temperature and

salinity related to habitat suitability; and two different components of the mangrove forest (edge and in-forest) related to the nature of mangrove habitats. Between 21 February and 1 March 2017, near-bottom (~ 5 cm above the sediment) DO (% saturation) and water temperature (°C) were measured every 15 minutes at each site using calibrated multi-parameter loggers (YSI Pro ODO model (accuracy ± 1 % saturation). A depth logger (In-Situ Inc. Rugged Troll 100 model) was coupled with each multi-parameter logger to measure water depth (cm) every 15 minutes. Salinity was measured every 15 minutes from 21 to 23 February, and between 28 February to 1 March 2017 using another multi-parameter logger (YSI 6920 V2-2) positioned at site 5. Tidal range was obtained from the SHOM website (SHOM, 2017).

4.2.3 Data extraction from videos

Methodological details to extract data from the videos are reported in Chapter 3. Briefly, as considerable time is required to process videos, I subsampled the acquired recordings. One neap tide and one spring tide sampling were randomly selected for processing. Five sites from the second neap and spring tide sampling were also processed so one randomly selected replicate on the reef platform (site 9), and two replicates of randomly selected paired sites, not located on the reef platform, were acquired (sites 5-8). Videos were viewed using VLC and subdivided in 5-min intervals to follow the temporal variations in fish assemblages. All taxa observed in each 5-min interval were identified and recorded. Only presence/absence data were recorded to avoid biases induced by count data when using UVCs (Sheaves et al., 2016). Fish were identified to the lowest possible taxonomic level, with all fish identifications validated by two additional experts. For each 5-min interval video, information about depth, DO, time of day, lunar phase (neap vs spring), habitat (edge vs in-forest), and tide direction (flooding vs ebbing) was recorded.

4.2.4 Data analysis

All data collected during the study on depth, DO, temperature and fish observations were collated into a unique dataset available as an appendix to this chapter. To graphically

investigate temporal dynamics of DO on the edge and in-forest, and covariance with depth and temperature, cubic spline smoothers were fitted to the three time series (DO, depth and temperature data collected every 15 minutes during 8 days) using R. DO residuals were graphically added to emphasise extreme DO levels. Despite the proximity between edge and in-forest sites of a same pair (within 5 m), it was expected that DO would be lower inside the forest due to the strong accumulation of organic matter. To test this hypothesis, a Kendall's correlation test (as DO did not follow a normal distribution) was used to determine whether patterns of change in DO were significantly correlated between edge and in-forest sites. Cumulative DO frequency curves (Chapter 2) were plotted for each site to highlight differences in spatial and temporal dynamics.

Following the methodology described in 3.2.3 Chapter 3, an index depending on observation per unit effort (OPUE) was used to calculate frequencies of occurrence for each taxa (the total number of 5-min intervals in which a taxon was observed in one sample unit was divided by the total number of 5-min intervals recorded for the same sample unit). I acknowledge the existence of non-independence issue created by subsampling videos in 5-min intervals. Indeed, this can potentially lead to the count of the same individual fish in sequential time windows. However, the objective here was to characterise environmental conditions suitable for the utilisation of mangrove habitats through time by different taxa. Therefore, I assumed that if an individual of a taxon was present (no matter if it was the same individual or another one to any recorded in previous 5-min intervals), then conditions were suitable. Frequencies of occurrence were first calculated per site. Only taxa with a frequency of occurrence ≥ 0.05 on at least one site were retained for analyses (hereafter referred to as "common taxa").

I hypothesised that presence of fish is partly driven by DO. To test this hypothesis, a random forest (RF) model (Breiman, 2001) was used to quantify the relative importance of DO and the other measured environmental factors, and identify how well the combination of the selected environmental factors predicted fish taxonomic richness. This machine learning algorithm permits analysis of data that do not meet the requirements of normality and

homoscedasticity required for approaches such as general linear models, and include repeated measurements (Mercier et al., 2011). The taxonomic richness (ranging from 0 to 13 taxa recorded within 5-min interval) was determined for each 5-min interval recorded (1434 5-min intervals in total). The dataset (available as a DOI: http://doi.org/10.25903/5cd4d312cbcfb) was then split in two to obtain a training dataset (875 5-min intervals obtained from the two entire sampling days processed) to build the RF model, and a test dataset (559 5-min intervals obtained from the 5 replicate sites processed) to test the robustness of the model at predicting taxonomic richness. The RF model, consisting of 1000 regression trees generated using 2 predictors at each split (default value), was created to predict taxonomic richness, with “Habitat” (edge vs in-forest), “Depth”, “DO”, “Lunar phase” (neap vs spring), “Time of day” (morning vs afternoon), and “Tide direction” (flooding vs ebbing) as predictors. The out-of-bag error estimate was used to validate the model. The increase mean-square error was calculated to determine the variable importance in predicting taxonomic richness, i.e. its predictive power, defined by the percentage of variability in the model explained by each variable. The model was then run on the test dataset to generate a confusion matrix. From the confusion matrix, the percentage of cases when the model was able to predict the exact taxonomic richness observed was calculated, as well as the percentage of cases where the model was able to predict the taxonomic richness observed at ± 1 taxon. All RF model-related analyses were conducted using the ‘randomForest’ package in R (Breiman, 2001). As a RF model is built from many classification trees, it is not accurate to draw a single tree from this model. Therefore, a univariate classification tree analysis was carried out on the training dataset with the same variables as the RF, and the tree obtained from this analysis was used to visually interpret the RF model. The univariate classification tree analysis was performed using the package “party” in R (Hothorn et al., 2010).

After quantifying the importance of DO, the goal was to understand when fish initiated responses to DO. Each 5-min video interval was allocated to a DO % saturation class in 10 % intervals (from 30-40 % saturation to 100-110 % saturation) according to the DO level recorded. The frequency of occurrence of each common taxon per class of DO was then

calculated to investigate whether intensity of utilisation varied in response to DO. A General Additive Mixed Model (GAMM) was built with $\log_{10}(X + 1)$ transformed frequencies of occurrence of each common taxon as the response variable, “DO” as a smooth term, and “Habitat” (edge vs in-forest) as a parametric term, using a Gaussian distribution and an identity link function. The model was built using the package “mgcv” in R (Wood, 2007). Frequencies were $\log_{10}(X + 1)$ transformed to reduce the impact of extreme values and improve visualisation. The frequencies of occurrence of each common taxon across DO were also plotted individually using a LOESS curve. Patterns were then investigated individually and visually grouped by similarity of mangrove utilisation in response to DO. No grouping was imposed, and visualisation of the data identified three common patterns of mangrove utilisation across DO among all common taxa. These three patterns were based on distinct preferences for DO with taxa recorded from 30 to 110 % saturation, taxa recorded from 50-110 % saturation, and taxa recorded from 70 to 110 % saturation.

Taxa observed in mangrove habitats even at low DO (from 30 to 110 % saturation) may indicate that these fish are well adapted to use mangrove habitats extensively and therefore expected to be observed more frequently than the other taxa. To test this hypothesis, overall frequencies of occurrence were calculated for each common taxon by dividing the total number of 5-min intervals in which a taxon was observed by the total number of 5-min intervals recorded during the study at the DO range corresponding to that taxon’s assigned pattern of utilisation (30-110 % saturation; 50-110 % saturation; 70-110 % saturation). Following this methodology allows to calculate frequencies of occurrence according to the effective sample size; it therefore overcomes the unbalanced sampling effort as species recorded across the entire range of DO would automatically be more frequent than species only recorded from 70-110 % saturation as it represents a smaller proportion of the sample size. Species-specific overall frequencies of occurrence were then plotted by type of patterns of utilisation assigned using boxplots. To test for differences in overall frequencies of occurrence among the different types of patterns of utilisation, a Kruskal-Wallis test followed by a post-hoc Dunn’s test were performed (data did not follow a normal distribution).

4.3. Results

DO was highly variable at the mangrove study sites in Bourake (Figure 16). DO reached levels as low as 14 % saturation at night low neap tides during the entire logging period, and as low as 35 % saturation during the morning hours that coincided with low spring tides while UVCs were deployed (Figure 16; Table 4). DO closely followed the diel- and tidal cycles, with daily maximum levels recorded during the afternoon high tide, and minimum levels during the night or early morning low tide. Temperatures followed a typical diel cycle, peaking during the late afternoon and declining at night reaching minimum levels in the early morning hours. Salinity was relatively constant during the study, ranging between 32.1 and 34.9.

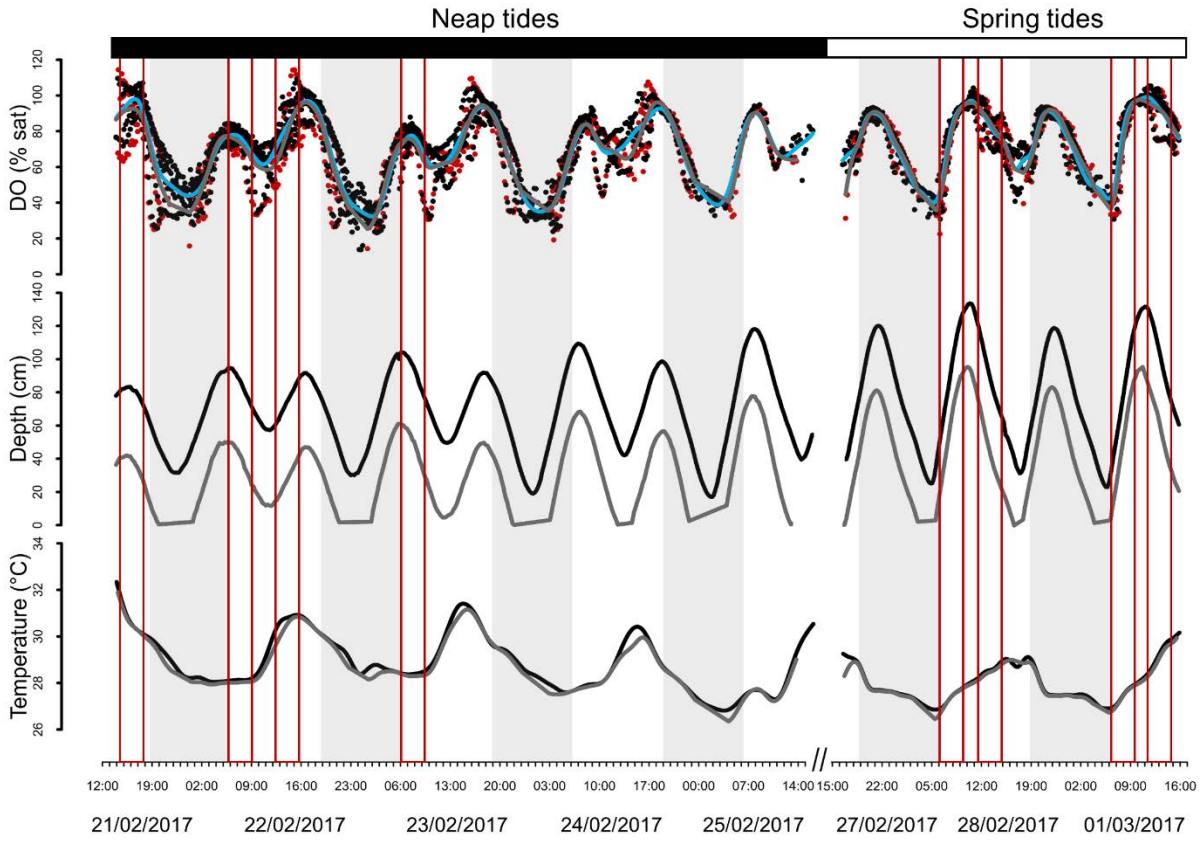


Figure 16 Cubic spline smoothers for dissolved oxygen (DO), depth and temperature. Data are from the 21 February to 25 February 2017 and from the 27 February to 1 March 2017. For DO, edge sites are represented by the blue smoother and black points, and in-forest sites by the grey smoother and red points. For the other factors, edge sites are represented by the black lines and in-forest sites by the grey line. Shaded areas represent sunset to sunrise. Each red box represents a UVCs sampling.

Table 4 Summary of the environmental factors during the study period.

Values	Neap	Spring

Environmental factors		Edge	In-forest	Edge	In-forest
DO (% saturation)	Min	13.7	14.3	30.9	22.6
	Max	110.6	114.4	105.5	103.3
	Mean (± SE)	67.2 (± 0.6)	71.4 (± 0.6)	76.8 (± 0.7)	79.5 (± 0.7)
Temperature (°C)	Min	26.2	25.8	25.9	25.1
	Max	32.0	31.5	30.5	30.4
	Mean (± SE)	29.1 (± 0.0)	28.9 (± 0.0)	28.0 (± 0.0)	28.0 (± 0.0)
Water depth (cm)	Min	1.1	0.0	2.4	0.0
	Max	118.1	77.8	133.7	95.5
	Mean (± SE)	55 (± 0.7)	34 (± 0.6)	71 (± 1.2)	48 (± 1.1)
Tidal range (m)	Min	0.35	0.35	1.25	1.25
	Max	0.59	0.59	1.38	1.38
	Mean	0.46	0.46	1.31	1.31

For each factor, the minimum, maximum and mean (± SE) values are provided for neap tides and spring tides, on the edge and in-forest sites.

Temporal dynamics in DO were significantly correlated between in-forest and edge habitats ($p < 0.0001$; $r = 0.95$; Figure 16; S5 Appendix). DO minima and maxima were also similar between edge and in-forest sites (Table 4). Most DO levels were between 70 and 80 % saturation, nevertheless, DO levels were equal or below 50 % saturation (adopted threshold for hypoxia; Chapter 2; Breitburg, 2002) for around 11 % of the time inside the forest and 21 % on the edge (Figure 17). Mean and minimum DO levels were lower during neap tides than spring tides for both edge and in-forest sites (Table 4). The duration of low DO tended to increase with distance from the mouth of the channel, with DO at or below 50 % saturation 4 % of the time at the in-forest site closest to the channel entrance (site 2), and 14 % of the time at the in-forest site furthest from the channel entrance (site 8; Figure 17).

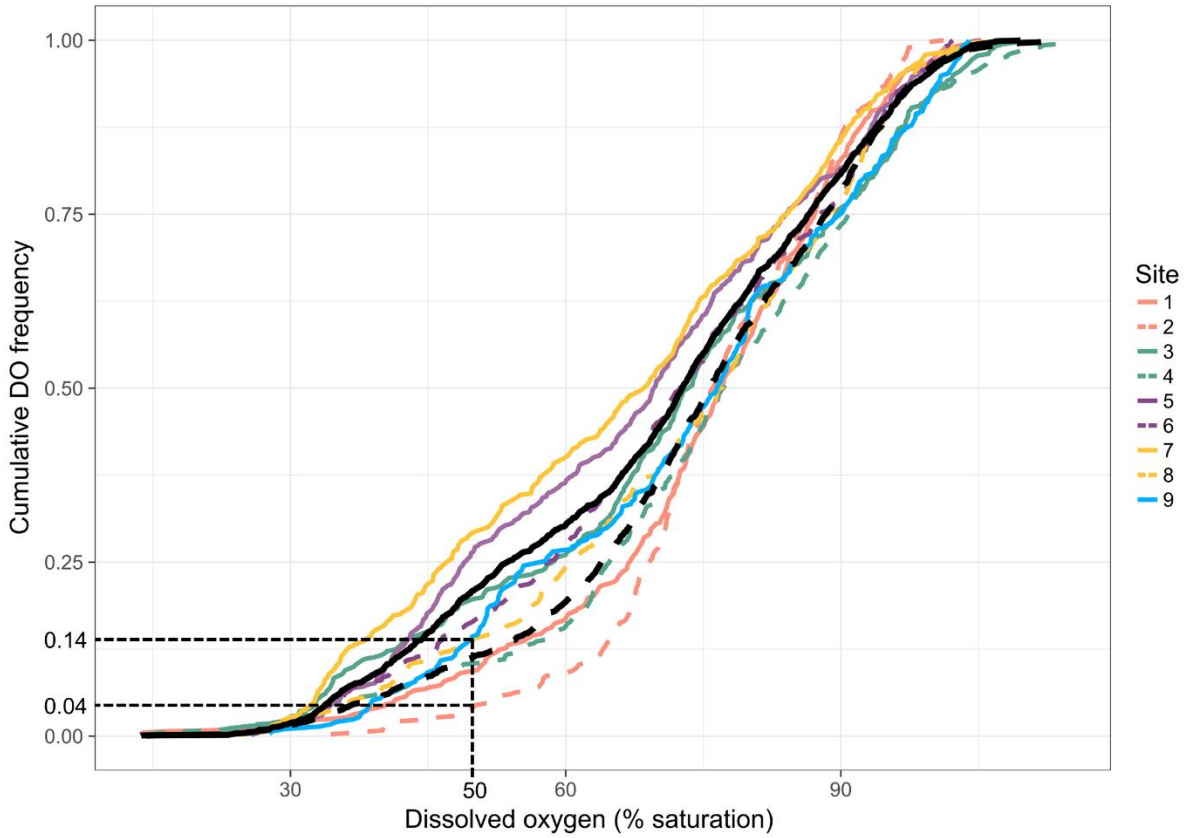


Figure 17 Site-specific cumulative DO frequencies.
Each colour represents a paired site (edge and in-forest), and edge sites are represented by solid coloured lines and in-forest sites by dashed coloured lines. The solid black line indicates the mean cumulative DO frequencies across edge sites and the dashed one the mean cumulative DO frequencies across in-forest sites. The frequency of hypoxia (DO ≤ 50 % saturation) at sites 2 and 8 is indicated to help read the figure.

Fifty-six video deployments were processed (totalling more than 118 h of video). Seventy-two taxa from 29 families were recorded, with 36 common taxa (frequency of occurrence ≥ 0.05) retained for further statistical analyses (Table 5). The full list of taxa identified is provided in Chapter 3.Table 3.

Table 5 The 36 common fish taxa identified by underwater video cameras at Bouraké, New Caledonia.

Family	Taxon
Acanthuridae	***Acanthurus auranticavus*** [1]
	Acanthurus grammoptilus [3]
Apogonidae	***Fibramia lateralis*** [1]
Carangidae	*Caranx papuensis* [1]
Chaetodontidae	***Chaetodon auriga*** [1]
	Chaetodon bennetti [1]
	Chaetodon lineolatus [1]
	Chaetodon lunula [3]
Lethrinidae	***Lethrinus harak*** [2]
	Lethrinus lentjan [3]
Lutjanidae	***Lutjanus argentimaculatus*** [1]
	Lutjanus fulviflamma [1]
	Lutjanus fulvus [1]
	Lutjanus russellii [1]
Monodactylidae	***Monodactylus argenteus*** [1]

	Chaetodon vagabundus [3]	Mugilidae	**Mugilidae spp.**[1]
	Heniochus acuminatus [3]	Mullidae	*Mulloidichthys flavolineatus* [1]
Clupeidae	Clupeidae spp. [3]		*Parupeneus indicus* [3]
Gerreidae	***Gerres oyena*** [2]		*Upeneus tragula* [2]
Gobiidae	*Amoya gracilis* [1]	Pomacanthidae	*Pomacanthus sexstriatus* [3]
	Asterropteryx sp. cf *striata* [1]	Pomacentridae	*Neopomacentrus* spp. [1]
	Cryptocentrus leptocephalus [3]	Scaridae	*Scarus* sp. cf *ghobban* [3]
	Gobiidae spp. [1]	Siganidae	*Siganus canaliculatus* [2]
	Redigobius balteatus [1]		***Siganus lineatus*** [1]
Haemulidae	*Plectorhinchus* spp. [2]	Sparidae	*Acanthopagrus* sp. cf *akazakii* [2]
	Pomadasys argenteus [2]		

The superscript number corresponds to the type of patterns of mangrove habitat utilisation across DO followed by the taxon (Figure 20). Taxa *highlighted in bold represent the 10 most common taxa. Taxa recorded in-forest (5 m inside the forest) are underlined.*

I used a RF model to assess the relative importance of several environmental factors in determining taxonomic richness. The robustness of the model in predicting taxonomic richness at this location was also tested. The RF model consisted of 875 5-min intervals and 6 independent environmental factors. It explained 50.2 % of the total variance in taxonomic richness, which considering the biological nature of the data is substantial. “Depth” had the highest predictive power for predicting taxonomic richness with its exclusion from the model increasing the mean-square error (MSE) by more than 61 % (Figure 18a). “Lunar phase”, “DO” and “Habitat” had similar predictive power (between 45 and 55 % increase in MSE) and explained a substantial part of taxonomic richness variability. “Time of day” and “Tide direction” had a lower predictive power but still accounted for an increase in MSE of more than 35 %. The RF model successfully predicted the exact taxonomic richness observed on the replicate sites for 23 % of the 5-min intervals recorded, and for 60 % of them at ± 1 taxon (S7 Appendix). As DO and depth were highly correlated, a RF model was built only with “Depth”, and then only with “DO” to test for the effect of multicollinearity on their relative predictive power. In both cases, the total variability explained by the model was much lower (33.42 % with only “Depth” included and 26.36 % with only “DO” included) than when “Depth” and “DO” were both included (50.22 %). The univariate tree corroborated the results of the RF in terms of variable importance, and proved to be an effective way of getting a visual interpretation of the RF (Figure 18b). The taxonomic richness was the lowest at in-forest sites, and on the edge

during spring tides. Conversely, taxonomic richness was the highest when water depth was the deepest during neap tides, and when DO was greater than 83 % saturation.

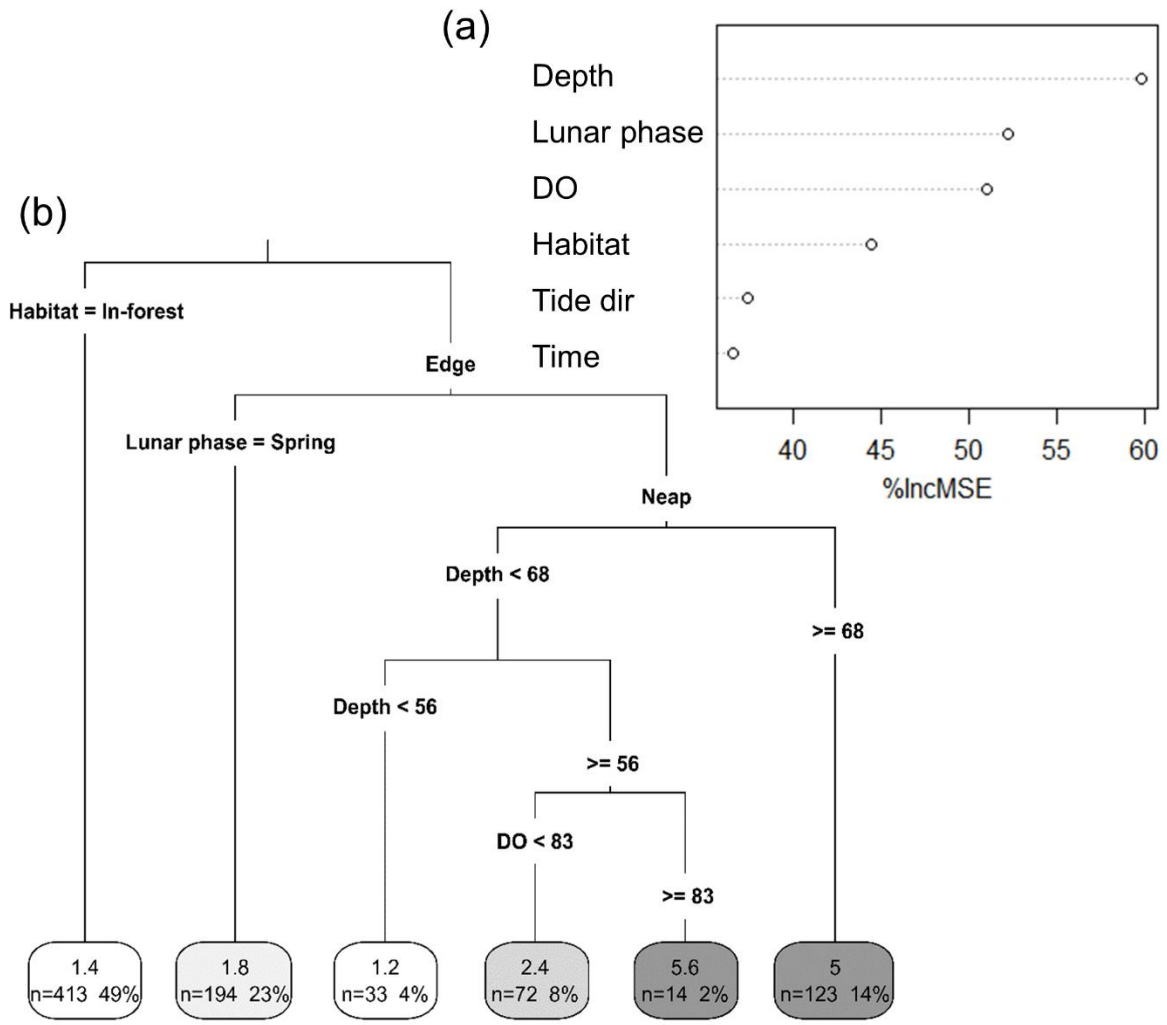


Figure 18 Importance of environmental factors in explaining variations in taxonomic richness. (a) Random forest importance plot. Importance plot was obtained from a random forest model built with Site, Depth (cm), Lunar phase (neap vs spring), DO: Dissolved oxygen (% saturation), Time: Time of day (morning vs afternoon), Tide dir: Tide direction (flooding vs ebbing) and Habitat (in-forest vs edge) as predictors for taxonomic richness. (b) Univariate classification tree. The tree was built using the same variables and provides a visual interpretation of the random forest model. Numbers in the boxes in each terminal leaf represent the average taxonomic richness, the number of samples (n), and the total % of data that n represents.

The RF model showed that DO was a key factor in explaining variations in taxonomic richness. I therefore further investigated fish responses to DO. Log_{10} transformed frequencies of occurrence of all taxa combined varied significantly across DO (GAMM: $F = 3.693$; $p = 0.0166$) and differ between habitat (GAMM: $F = 11.48$; $p < 0.0001$). On average, frequencies of occurrence were highest once DO reached 70-80 % saturation (Figure 19). The spread of

the frequencies of occurrence around the median was also substantially reduced once DO was between 70 and 110 % saturation, indicating that taxa were more equally frequent, whereas at low DO levels only a few taxa were abundant, with the rest rarely observed, or absent entirely. The patterns of utilisation across DO intervals differed between the in-forest and edge habitat (Figure 19). Although, on average, the highest frequencies of occurrence were recorded once DO reached 70-80 % saturation for both habitats, there were larger disparities between taxa at edge sites, with some being frequently observed at low DO and some being rarely observed, or absent entirely until DO reached 70-80 % saturation (Figure 19a), while at in-forest sites, frequencies of occurrence were more stable across DO (Figure 19b).

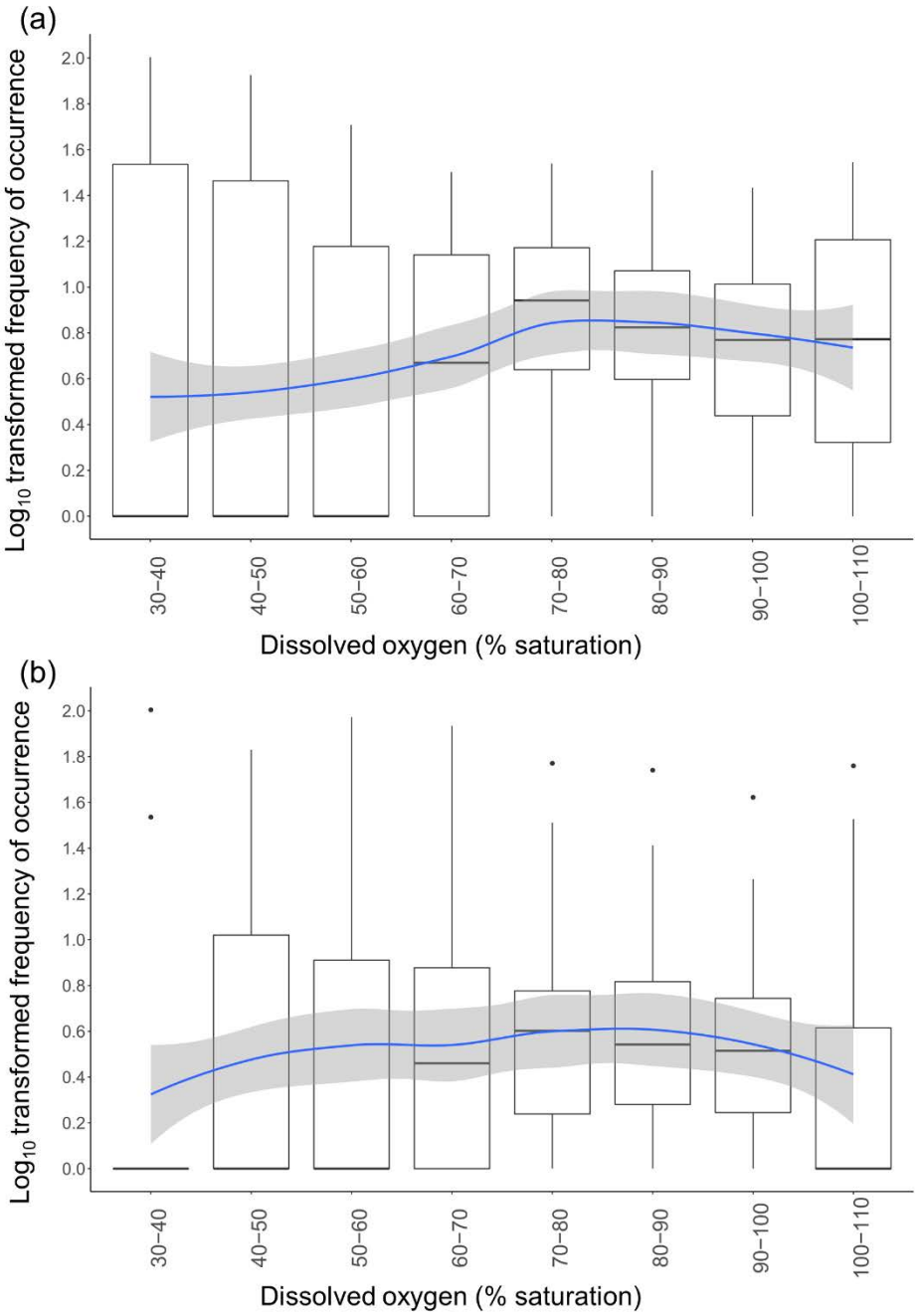


Figure 19 Variation in frequencies of occurrence of fish across DO.
Frequencies of occurrence were log10 transformed. Each data point used to draw the boxplots represents the frequency of occurrence of one common taxon during a specific DO class. The blue line represents the GAMM model fitted with DO as the smooth term using a Gaussian distribution and an identity link function for (a) Edge sites; and (b) In-forest sites. Shaded areas represent the confidence interval at 95 %.

Disparities in frequencies of occurrence between taxa were explained as fish appeared to respond differently to DO fluctuations. I identified 3 distinct types of patterns of mangrove utilisation across DO while investigating species-specific variations in frequencies of occurrence across DO: 1) Pattern 1: *"High tolerance"* – these taxa (19 taxa) were recorded

across the entire range of DO (30-110 % saturation) and were usually known to use mangrove habitats extensively (Figure 20; Table 5; S6a, b Appendix); 2) Pattern 2: "*Medium tolerance"* – these taxa (7 taxa) were not observed once DO was below 50-60 % saturation and were also usually known to use mangrove habitats extensively (Figure 20; Table 5; S6c Appendix); and 3) Pattern 3: "*Low tolerance*" – these taxa (10 taxa) were not observed once DO was below 70-80 % saturation and were usually reef-associated taxa (Figure 20; Table 5; S6d Appendix). Figure 20 only shows one example of taxa per type of patterns, however, all the species-specific patterns are provided in S6 Appendix.

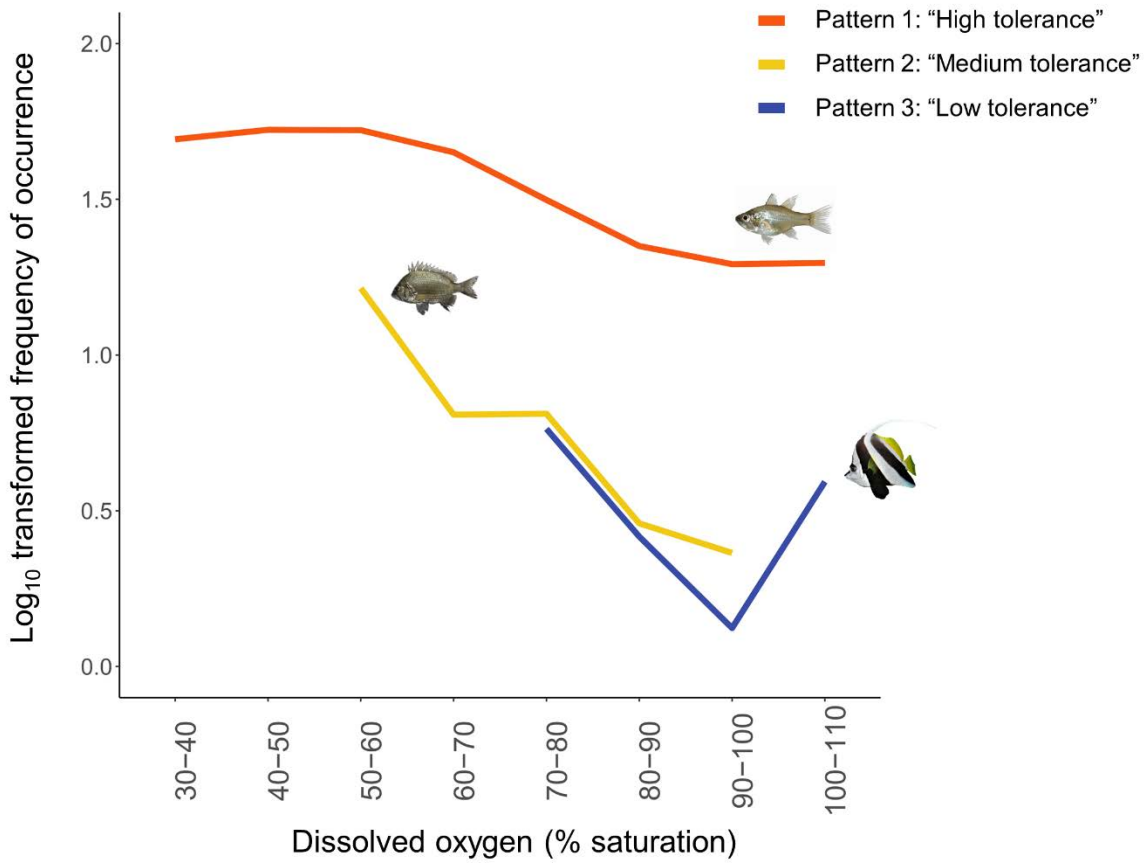


Figure 20 The three common patterns of mangrove utilisation across DO identified.
Each LOESS curve represents one example of taxa per type of patterns of mangrove utilisation across DO: Pattern 1: "High tolerance" represented by taxon Fibramia lateralis; 2) Pattern 2: "Medium tolerance" represented by taxon Acanthopagrus sp.; 3) Pattern 3: "Low tolerance" represented by taxon Heniochus acuminatus. LOESS curves were built with the log10 transformed frequencies of occurrence.

The type of patterns followed by a taxon and its overall frequency of occurrence appeared to be significantly correlated (Figure 21; Kruskal-Wallis: $\chi^2 = 9.8757$; $p < 0.01$). Taxa following a *"High tolerance"* pattern were on average significantly more frequently observed

than taxa following a "*Low tolerance"* pattern (Dunn's test: $p < 0.01$). Overall frequencies of occurrence of taxa following a "*Medium tolerance*" pattern were intermediate but not significantly different than "*High tolerance*" taxa (Dunn's test: $p > 0.5$) or "*Low tolerance*" taxa (Dunn's test: $p > 0.1$).

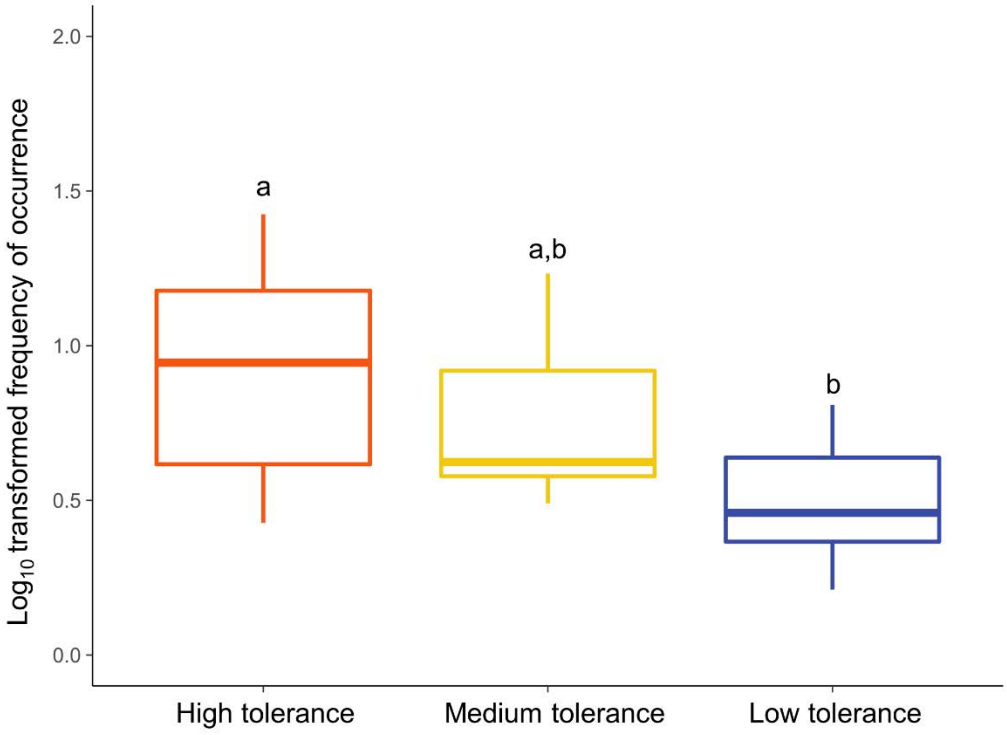


Figure 21 Relationship between frequencies of occurrence and type of patterns followed. Overall frequencies of occurrence were calculated for each common taxon at the DO range corresponding to that taxon's assigned pattern of utilisation. Differential letters above boxes denote statistically different values between patterns of utilisation (Dunn's test: $p < 0.05$).

4.4. Discussion

4.4.1 Tidal migrations: stranding or hypoxia?

Fish assemblages were shown to be highly variable over time and space in the study area (Chapter 3). About half of this variability was explained by multiple environmental factors among which depth, DO, lunar phase, and location within the mangrove forest (edge or in-forest) had the highest predictive power. The main trend identified among the temporal variability in fish assemblages occurred at a tidal scale (Chapter 3). This highlights that fish were responding to one or several factors covarying with tide. Tidal variations in fish assemblages are common in intertidal environments (Laroche et al., 1997; Ellis and Bell,

2008; Becker et al., 2012), however, the factors responsible for their occurrence have rarely been investigated. There was a high collinearity between depth and DO as both varied across the tidal cycle, and the importance of these two factors to explain variations in fish assemblages was high. Consequently, it is likely that depth and DO play an essential role in triggering tidal migrations. Previous studies have shown that fish can respond to both water depth and DO changes (Wannamaker and Rice, 2000; Bretsch and Allen, 2006; Johnston and Sheaves, 2007; Rountree and Able, 2007; Ellis and Bell, 2008; Brady and Targett, 2013), emphasising the idea that fish could be using depth and DO interchangeably as cues to initiate tidal migrations, a trigger that might be dependent on the perceived upcoming risk (stranding or hypoxia).

Depth becomes limiting when fish cannot safely access the area because it is too shallow, with associated risk of stranding. However, many taxa, including small sized species, avoided mangrove habitats even when they potentially had enough water (Chapter 3). On the other hand, changes in DO can rapidly impair fish fitness (Chabot and Claireaux, 2008; Vaquer-Sunyer and Duarte, 2008). Indeed, in aquatic environments, DO is considered as the primary limiting factor (Fry, 1971; Claireaux and Chabot, 2016) as it is naturally scarcer than in the atmosphere (Diaz, 2001), making it a perpetual challenge for fish to access available oxygen in the water. In the mangrove forest examined here, changes in DO across tide were extreme, with up to 80 % loss during one tidal period (high to low), supporting the notion that DO could be a critical constraint for fish to access mangrove habitats, even when depth is suitable. Considering the relevance of both factors, and the fact that the risk of stranding and hypoxia are concomitant, it is likely that fish are adapted to respond to either depth or DO, depending on which one becomes limiting first, and this may vary among taxa.

The hypothesis that fish can interchangeably respond and tolerate adverse depth and DO conditions was supported by the fact that all taxa that access mangrove habitats at low depth in Bourake (Pattern 3: “Low-depth users”; Chapter 3) were all following a “*High tolerance*” pattern here in response to DO, indicating that they were able to tolerate low depth as well as low DO. The effects of depth and DO might well be mostly confounded as DO

fluctuations overall follow depth, however, DO amplitude (difference between minimum and maximum levels) depends on many interacting factors including weather (Tyler et al., 2009), local geomorphology or biological and chemical activities (Mazda et al., 1990; Peña et al., 2010). Therefore, minimum and maximum DO levels for a same depth can differ and vary in complex spatial and temporal scales, independent from the tidal scale, probably explaining why the predictive power of both depth and DO was high. These results emphasise the importance to understand the DO dynamics and its impacts on fish to comprehend how mangrove forests are being used.

4.4.2 Tidal-induced dissolved oxygen variations

During this study, I hypothesised that DO could be a keyt limiting factor for fish utilising intertidal mangrove forests, and my findings support this hypothesis. However, the associated risk of hypoxia in the study system was still to be tested. Diel-hypoxia conditions observed in other mangrove systems (Chapter 2; Knight et al., 2013; Gedan et al., 2017; Mattone and Sheaves, 2017) was also a seemingly common condition in Bourake. DO showed extreme and rapid fluctuations with the diel and tidal cycles. Low DO was recorded daily during nighttime when the tide was ebbing, reaching levels that can compromise fish fitness (Rogers et al., 2016). It is likely that hypoxia is a common condition of intertidal mangrove forests due to the mineralisation of a large amount of organic matter produced by mangrove trees, responsible for a high consumption of oxygen by bacteria (Alongi et al., 2004a; Dittmar et al., 2006), but also due to the exchange of porewater between sediments and water column, known as “tidal pumping” (Li et al., 2009; Gleeson et al., 2013; Call et al., 2015; Leopold et al., 2017). Briefly, at each flooding tide, water infiltrates intertidal sediments and then drains back to the water column during the next ebbing tide. While in the sediments, water becomes enriched in reduced compounds such as NH_3, H_2S, FeS_2, resulting in water acidification and deoxygenation (Marchand et al., 2011). As porewater accumulates in the water column throughout ebbing tide (Bouillon et al., 2007), it drives extreme drops of oxygen usually observed at low tide. Connectivity with the Pritzbuer Bay was crucial here in this mangrove-

coral semi-enclosed lagoon as the flooding tide presumably brings oceanic water that is more saturated, replenishing DO levels. During spring tides, higher DO levels were recorded, probably driven by higher water renewal compared to neap tides. There was no difference observed between DO dynamics on the edge and in-forest, however minimum values were slightly lower on the edge because water remained permanently at low tide being subjected to further decline compare to in-forest that became exposed earlier during the tide and therefore experiencing a shorter DO decline period.

4.4.3 Species-specific responses to DO variations

Fish significantly responded to DO variations, with taxonomic richness and average frequencies of occurrence higher and more consistent once DO reached 70-80 % saturation. This result indicated that DO levels reached during the study were probably low enough to cause harmful effects, and therefore, many taxa responded by temporarily avoiding the area. Apparent behavioural avoidance thresholds observed were species-specific and were initiated at different DO levels, potentially driven by differential tolerances to low DO (Claireaux and Chabot, 2016). Three main types of patterns of mangrove utilisation were identified driven by taxa's behavioural avoidance thresholds. Most taxa did not display any behavioural avoidance ("*High tolerance*" pattern), and some of these taxa even reached their maximum frequency of occurrence at the lowest DO levels recorded (30-40 % saturation). Most of these taxa are known to commonly use mangrove habitats such as *L. argentimaculatus*, Mugilidae spp., and Gobiidae spp. (Froese and Pauly, 2017). On the other hand, other taxa were not observed either below 50-60 % saturation ("*Medium tolerance*" pattern), or below 70-80 % saturation ("*Low tolerance*" pattern). Taxa following a "Low tolerance" pattern, were mostly reef-associated species, and therefore are not usually seen in mangrove habitats, such as *C. vagabundus*, *H. acuminatus*, and *Scarus* sp. (Froese and Pauly, 2017). The three different types of patterns of utilisation observed may highlight that taxa following a "*High tolerance*" pattern, and therefore taxa commonly seen in mangrove habitats, are more tolerant to low DO than taxa following "*Medium tolerance*" and "*Low tolerance*" patterns.

Even though the underlying adaptations behind these patterns still need to be investigated, these observations suggest that taxa able to withstand low DO appeared as the most successful at using mangrove habitats (more frequently observed and more abundant) over taxa displaying avoidance behaviour. Indeed, "*High tolerance*" taxa were on average more frequently observed than "*Medium tolerance*" taxa, themselves more frequently observed than "*Low tolerance*" taxa. Tolerance to low DO provides an evident benefit as taxa can use mangrove habitats more often and for longer periods compared to taxa that need to migrate temporarily to avoid harmful DO levels. Moreover, remaining in low DO when most other taxa must leave, can provide opportunistic feeding and limited competition (Diaz et al., 1992; Rahel and Nutzman, 1994). On the other hand, tidal migrations can have indirect costs as they can increase risk exposure to predators as fish travel to open water, aggregate fish in suboptimal habitats (less food, more predation) while waiting for DO conditions to improve, and increase energetic costs during extended swimming activities (Eby et al., 2005b; Shoji et al., 2005; Chabot and Claireaux, 2008; Craig, 2012). This implies that being adapted to withstand low DO might be critical for taxa using mangrove habitats extensively.

While no differences in DO levels were found between the edge and inside of the forest, it was interesting to note that most taxa venturing in-forest (23 taxa) were following a "*High tolerance*" pattern (16 taxa; 4 taxa were following a "*Medium tolerance*" pattern, and 3 taxa a "*Low tolerance*" pattern). In other mangrove forests, DO can reach levels close to 0 % saturation (Knight et al., 2013; Mattone and Sheaves, 2017), so it is possible that such lethal levels are also occasionally reached in Bourake. This could explain why relatively few taxa venture inside the forest, and those that do, appear to be highly tolerant to hypoxia.

4.5. Conclusions

The overall value of mangrove forests has been linked to parameters such as geographical location, tidal range (micro-, meso- or macrotidal), setting (coastal, estuarine, island, embayment), and connectivity to adjacent habitats (Unsworth et al., 2008; Igulu et al., 2014; Bradley et al., 2019). While these factors provide important information, this study also

shows that for a same mangrove forest, its value is temporally and spatially variable. About half of the variability in fish assemblages was explained by changes in depth, DO, lunar phase, position within the mangrove forest, time of day and tide direction. Most of the temporal variability occurred on a tidal scale, highlighting the importance of tide in driving mangrove forests utilisation. Here, depth and DO were mostly considered to explain tidal variations in fish assemblages, however, tide can induce variations in many other factors. For instance, a recent study suggested that the resuspension of mangrove-derived organic matter via porewater exchange could temporally boosts primary and secondary production, attracting fish regardless of water quality conditions (David et al., 2018). These results highlight the complexity to quantify the utilisation, and consequently, the value of mangrove forests and call for more investigations, especially on the effects of tide.

This study is the first to provide insights on how mangrove forests utilisation by fish is influenced by DO. It suggests that tolerance to low DO may be a widespread adaptation for taxa commonly using mangrove forests and could explain why they manage to thrive in these harsh environments. The need of being tolerant to low DO, or able to undertake tidal migrations while limiting alternative costs, is likely to limit the number of taxa using intertidal mangrove habitats that experience low DO. However, with only field data it is difficult to attribute specific fish responses to DO. Physiological techniques could be used to determine whether a difference in hypoxia tolerance could explain why some species access mangrove habitats at low DO levels while others access at higher DO levels (Lawton, 1991; McGill et al., 2006). This is the first study to look at, and suggest, a relationship between DO and fish utilisation of mangrove habitats. It adds to our knowledge on factors determining mangrove habitats value and highlights the importance to consider DO as a key controlling factor. More in-depth evaluation of DO dynamics and its impacts on fish populations in other locations would certainly help understanding the heterogeneous value of intertidal mangrove forests.

4.6. Summary

Tidal variations in fish assemblages recorded in chapter 3 were further investigated to identify the driving factors. Depth was identified as the most important factor to explain tidal variations. However, DO showed a high correlation with water depth, as DO is highly influenced by tide as demonstrated in chapter 2. Moreover, the minimum DO values recorded are commonly associated with adverse effects on behaviour and physiology. DO was also identified as a key factor in explaining tidal variations in fish assemblages. In-situ video observations reveal species-specific avoidance strategies in response to developing hypoxia. Taxa commonly using mangroves could withstand hypoxia while others usually associated with reef habitats were not recorded below 70 % saturation. These results suggest that being tolerant to low DO could be a required adaptation for the extensive use of mangrove forests.

Chapter 5 Mangrove habitats utilisation is related to species hypoxia tolerance

Prepared for submission in Functional Ecology

5.1. Introduction

5.1.1 Environmental hypoxia – why is it a problem?

Dissolved oxygen (DO) is considered the main limiting factor for marine aerobic organisms to perform all energy-requiring activities (Fry, 1947; Fry, 1971). Environmental hypoxia develops in aquatic environments as DO declines and aquatic organisms respond by modifying their behaviour (Kramer, 1987; Breitburg, 1994; Diaz and Rosenberg, 1995; Craig, 2012) and physiology (Greaney et al., 1980; Peterson, 1990; Breitburg et al., 1997; Wu, 2002; Zambonino-Infante et al., 2017). These responses lead to ecosystem scale impacts such as modifications of species distributions (Eby and Crowder, 2002), predator-prey interactions (Breitburg et al., 1994), and in severe cases, habitat loss and mass mortality (Townsend and Edwards, 2003; Chabot and Claireaux, 2008; Diaz and Breitburg, 2009). Environmental hypoxia has severe consequences on marine ecosystems and is therefore considered one of the most pressing threats for the ocean (Diaz and Rosenberg, 1995; Rabalais et al., 2010; Breitburg et al., 2018). The frequency and severity of hypoxia is expanding worldwide due to anthropogenic nutrient enrichment and is expected to further exacerbate in the context of climate change, placing further environmental pressure on marine ecosystems (Diaz and Rosenberg, 2008; Breitburg et al., 2018).

5.1.2 How do fish respond to hypoxia?

Fish elicit a range of behavioural and physiological responses to environmental hypoxia (Wu, 2002). Common behaviours involve avoidance of hypoxic areas, reduction of activity level, use of aquatic surface respiration and air-breathing strategies (Kramer, 1987; Chapman and McKenzie, 2009). Such responses occur often in addition to physiological

changes, such as increase in haemoglobin–O_2 binding affinity, blood haemoglobin content or gill surface area, that aim to enhance oxygen extraction and transportation in order to sustain metabolic needs for aerobiosis as DO rarefies in the surrounding environment (Richards, 2009; Wells, 2009; Rogers et al., 2016). Metabolic rate, measured through oxygen uptake, is a useful tool to estimate energy production, and therefore characterise species ecological performances (Chabot et al., 2016a). Species capacity for aerobic metabolism declines concomitantly with DO until the critical oxygen level (O_{2crit} or P_{crit}) is reached (Fry, 1971; Chabot and Claireaux, 2008). At O_{2crit}, maximum metabolic rate (MMR) is equal to standard metabolic rate (SMR), therefore only minimal cost of living can be sustained with no excess activity possible, such as swimming or digesting (Chabot et al., 2016b). Above the O_{2crit} short-term survival is not compromised, therefore the ability of fish to maintain aerobic metabolism as DO decreases is important in determining fish hypoxia tolerance (Claireaux and Chabot, 2016).

Capacity for survival at DO below O_{2crit} is also important in determining fish hypoxia tolerance. The ability to survive at DO below O_{2crit} is determined by the capacity of fish to maintain ATP supply through a combination of anaerobic metabolism and metabolic rate depression (Guppy and Withers, 1999; Richards, 2009). Fish can also develop physiological adaptations, such as high levels of tissue glycogen and changes in enzyme and protein expression, to improve anaerobiosis (Nilsson and Östlund-Nilsson, 2008; Richards, 2009; Speers-Roesch et al., 2013). As secondary wastes from anaerobiosis accumulate, fish may show acute signs of distress such as loss of equilibrium (LOE), indicating the limit to anaerobic capacity corresponding to the incipient lethal oxygen (ILO) level (Gaesser and Brooks, 1984; Claireaux and Chabot, 2016). Survival below O_{2crit} is a function of hypoxic severity and time, therefore time spent in DO levels below O_{2crit} is important to consider when quantifying hypoxia tolerance of fish (Nilsson and Östlund-Nilsson, 2008; Claireaux and Chabot, 2016).

5.1.3 Application of laboratory experiments to field observations

A causal link between environmental hypoxia and responses to hypoxia is difficult to establish using only field observations as fish rarely respond to changing DO only, but rather to a range of interacting stressors, such as high temperature, low pH, and toxins accumulation, that can generate similar responses (Wu, 2002; Vaquer-Sunyer and Duarte, 2008). Several studies have described a relationship between fish movements in estuaries and environmental hypoxia (Eby and Crowder, 2002; Bell and Eggleston, 2005; Tyler and Targett, 2007; Brady and Targett, 2010; Craig, 2012; Brady and Targett, 2013), however few studies have directly integrated such observations with empirical determinations of metabolic responses in controlled laboratory conditions. Metabolic adjustments play an important role in driving responses to stressors, hence, the integration of physiological responses observed in laboratory conditions with environmental DO and fish responses observed in the natural environment is crucial for predicting changes in fish communities (Lawton, 1991; Helmuth, 2009; Stoffels, 2015), and provide crucial information for conservation and management (Illing and Rummer, 2017). As metabolic adjustments are species-specific (Breitburg, 2002; Vaquer-Sunyer and Duarte, 2008; Rogers et al., 2016) and depend on the type of hypoxic environments fish live in (Mandic and Regan, 2018), existing knowledge cannot be extended to other species. Thus, species-specific characterisation of metabolic responses is needed when evaluating the potential impact of environmental hypoxia on fish communities inhabiting a particular hypoxic environment.

5.1.4 Hypoxia in mangroves

Mangroves are considered highly valuable habitats for fish (Nagelkerken et al., 2008), however the occurrence of diel-cycling environmental hypoxia, that may range from moderately to severely hypoxic and last for hours, suggests that they may be temporally unsuitable for some fish species (Chapter 2, Chapter 4, Mattone and Sheaves, 2017). Indeed, diel-cycling hypoxia in mangrove forests was shown to induce behavioural responses, that were indicated by species-specific variations in fish occurrence in relation to DO (chapter 4). Such responses may be the result of differential tolerances to hypoxia, leading to different

strategies in mangrove utilisation that are dependent on DO. Like in other hypoxic environments, it is likely that DO plays a key role in shaping mangrove fish communities depending on their hypoxia tolerance (Dauer, 1993; Eby and Crowder, 2002; Wu, 2002; Mandic et al., 2009). Despite the importance of mangroves for many fish species and the increasing evidence of hypoxia occurrence, little is known on hypoxia tolerance of mangrove fish species and the capacity of hypoxia to reduce mangrove habitat quality.

Here, I used existing knowledge on DO and fish occurrence in response to DO fluctuations from an Indo-Pacific mangrove forest to design laboratory experiments to characterise hypoxia tolerance of mangrove fish species. The results are used to examine whether a causal link between hypoxia tolerance and species-specific utilisation of mangrove forests exists. Four fish species were selected for this study: two that are commonly observed in mangrove forests, and two that are occasionally observed but are more commonly associated with adjacent coral reef ecosystems. Each of these four fish species has been observed to access mangrove forests at different DO ranges believed to be due to differential hypoxia tolerances. Metabolic responses to hypoxia were characterised for each of these four species using intermittent-flow respirometry. I hypothesised that the two species selected that are frequently observed in mangrove forests and at low DO (*Acanthopagrus pacificus* and *Siganus lineatus*), would be more tolerant to hypoxia than the two reef species that infrequently visit mangrove forests and are present only at high DO (*Chaetodon vagabundus* and *Heniochus acuminatus*).

5.2. Materials and methods

5.2.1 Study Species

Four species were selected for determination of metabolic responses to hypoxia, based on field data collected in a mangrove/coral system in New Caledonia (21˚56.971S, 165˚59.481E), revealing their contrasting patterns of mangrove utilisation in relation to DO. Golden-lined spinefoot, *S. lineatus* (Valenciennes, 1835) was following a “High tolerance” pattern: it had no apparent preference for DO and was frequent at the lowest DO levels

recorded (30-40 % saturation; Figure 22; Chapter 4). It was therefore chosen as a species potentially highly tolerant to hypoxia. Pacific seabream, *A. pacificus* (Iwatsuki et al., 2010), was following a "Medium tolerance" pattern: it was not recorded at DO below 50-60 % saturation but occurred frequently (Figure 22; Chapter 4) and was therefore selected as a species potentially medium tolerant to hypoxia. Pennant coralfish, *H. acuminatus* (Linnaeus, 1758) and vagabond butterflyfish, *C. vagabundus* (Linnaeus, 1758) were following a similar "Low tolerance" pattern of mangrove utilisation: they were not recorded at DO below 70-80 % saturation and were less frequently observed than the two other species (Figure 22; Chapter 4). Therefore, they were selected as species potentially low tolerant to hypoxia.

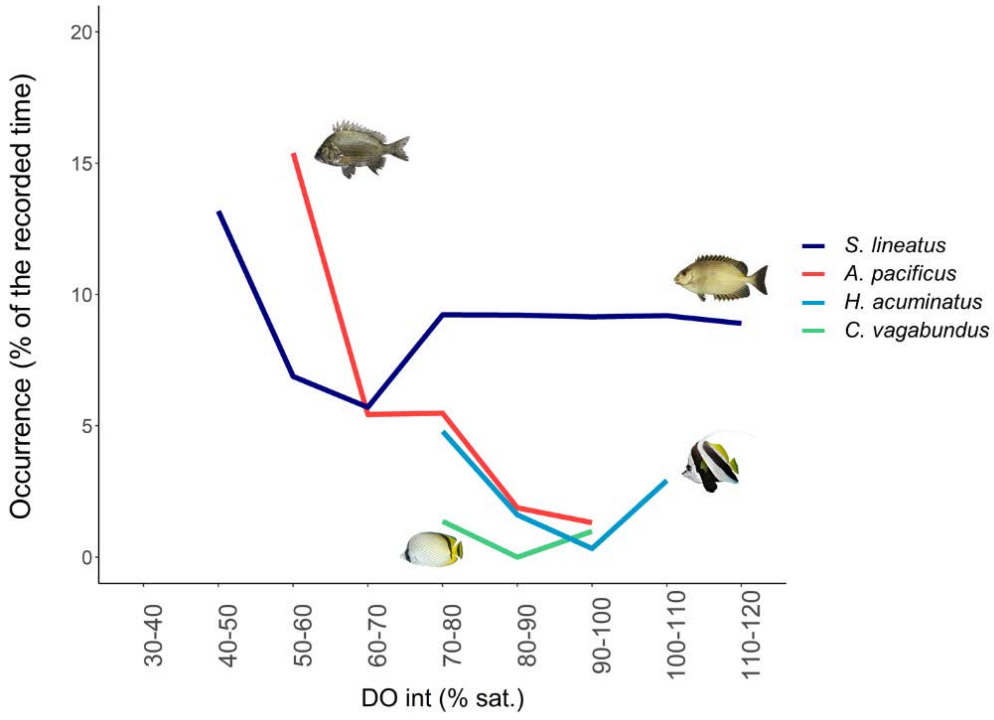


Figure 22 Occurrence of the four study species in relation to DO.
Occurrences were determined from a field study conducted in a mangrove/coral system in New Caledonia (Chapter 4). Fish were observed with underwater video cameras coupled with DO loggers. Occurrences represent the percentage of time a species was recorded over the sampling period (more than 118 h of video recording) at a specific DO int (dissolved oxygen interval).

Juvenile *A. pacificus* (0.021 – 0.137 kg, n = 20) and *S. lineatus* (0.021 – 0.164 kg, n = 15) were collected from the Ross River, Townsville, Australia (19°17'2.45"S, 146°48'53.80"E) using hook and line and cast net methods, respectively. *H. acuminatus* (0.200 – 0.250 kg, n = 15), and *C. vagabundus* (0.015 – 0.020 kg, n = 15), were professionally hand-caught in the

Coral Sea. Fish were maintained in multiple shaded outdoor 900 L flow-through tanks at James Cook University's Marine Aquarium Research Facilities Unit (MARFU). Tanks were continuously supplied with aerated, recirculating UV-filtered saltwater (salinity = 34 psu). Fish were maintained for a minimum of ten days post-capture to acclimate to captivity and the experimental temperature of 28 °C. This experimental temperature represents the average temperature recorded in mangrove habitats over summer months in New Caledonia and north Queensland, Australia (Chapter 2, Chapter 4). During this acclimation period, fish were fed twice daily *ad libitum* but were fasted 24 h prior to experimentation.

5.2.2 Respirometry

Oxygen consumption rate (O_2) measurements were completed using static intermittent-flow respirometry (Figure 2), following best practices highlighted by Svendsen et al. (2015). Three different sizes of acrylic custom-made chambers were used to fit the different sizes and shapes of the four species (10.5 L; 1.9 L; 1.1 L). Two to six chambers were submerged in a thermoregulated (28.4 ± 0.2 °C) and aerated 300 L experimental tank. Each chamber was connected to two submersible pumps: a flush pump that intermittently replenished water in the chambers between oxygen measurements, and a recirculation pump that continuously mixed water within the chamber. A timer was connected to the flush pumps to repeat an 8-minute measurement cycle that consisted of a 3-minute measurement period followed by a 5-minute flush period. DO within chambers was measured every 2 s using oxygen-sensitive REDFLASH® dye on contactless spots that was connected to the recirculation loop. Each oxygen sensors were connected to a four channel Firesting Optical Oxygen Meter (Pyro Science e. K, Aachen, Germany) via fibre-optic cables. Before each experiment, the oxygen sensors were calibrated to 0 % saturation (using a sodium sulfite solution) and 100 % saturation (using aerated seawater). The experimental tank was surrounded by an opaque curtain and the individual chambers were fitted with opaque covers to minimise stress caused by visual stimuli.

Fish were transferred individually to the chambers using scoop nets and plastic bags to limit stress induced by air exposure. Fish were left undisturbed for around 70 h at normoxia (> 80 % saturation) to acclimate to the chamber environment and for subsequent determination of SMR. To validate the applicability of my laboratory results, DO was slowly decreased for about 6 h, from 100 % saturation until fish lost equilibrium (rate of around 20 % saturation per hour), to simulate natural conditions in mangrove habitats harbouring the four species tested (Figure 23), using nitrogen gas connected to a degassing column. LOE was deemed to have occurred when a fish was no longer able to elicit a righting response. At LOE, both time and DO were recorded and fish were removed from the chamber, wet weighed, measured, and transferred to a recovery tank with 100 % saturated water. DO measurements were recorded in all chambers for 30 min before and after introduction of fish for subsequent determination of background respiration. To limit bacterial growth, all respirometry equipment (experimental tank, degassing column, chambers, connecting pipes and pumps) was bleached following the completion of each trial and the experimental tank was continuously supplied with UV-filtered seawater until the beginning of the hypoxia challenge. Data exploration showed that any change in background respiration between the start and end of experiments was better explained by an exponential model, therefore an exponential relationship was fitted when correcting fish O_2 for background respiration.

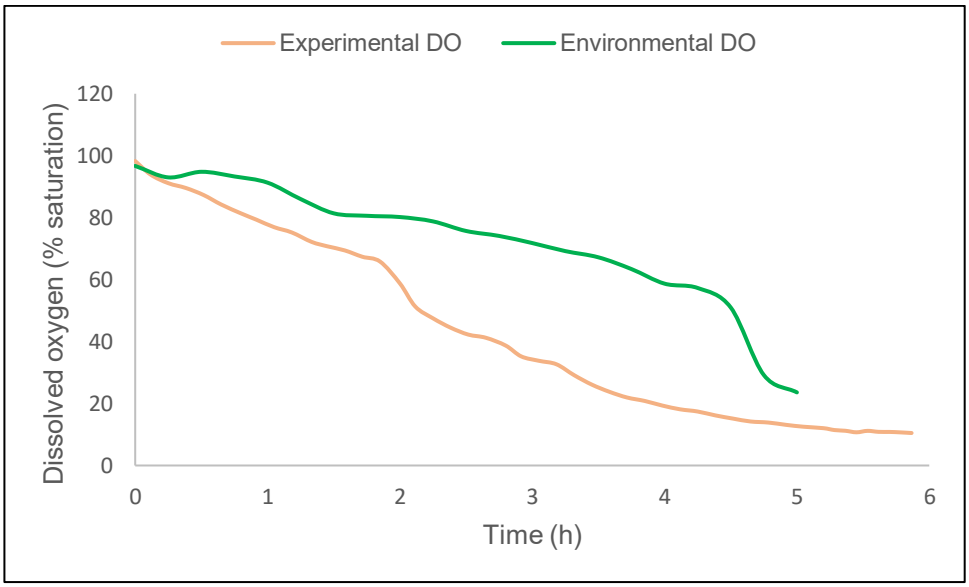


Figure 23 Rates of DO decline in the natural environment and during the experiments.

The green curve represents a typical DO profile obtained in the field in Bourake, New Caledonia, and the orange curve represents a typical DO decline applied during the respirometry trials.

5.2.3 Calculations and Statistical Analysis

All oxygen consumption rate measurements (O_2 in $mgO_2.kg^{-1}.min^{-1}$) were calculated from the slope of the decline in oxygen concentration according to the following formula (Steffensen, 1989; Collins et al., 2013) using the commercial software LabChart v. 8.1.10 (ADInstruments, Sydney, NSW, Australia):

$$\dot{M}O_2 = \frac{[(slope_a * 60) * (V_c - M_b)] - [(slope_b * 60) * V_c]}{M_b}$$

where $slope_a$ was the decline in oxygen ($mg.L^{-1}.s^{-1}$) in the presence of the fish, $slope_b$ was the decline in oxygen ($mg.L^{-1}.s^{-1}$) in the absence of the fish (background respiration), V_c and M_b are the volumes (L) of the chamber and the fish, respectively. Only slopes with an $R^2 > 0.90$ were included in this analysis.

Four parameters were calculated from the O_2 measurements to determine hypoxia tolerance for the four species (Figure 3): O_{2crit} (DO below which the fish is not able to maintain SMR); $O_{2deficit}$ (the amount of O_2 consumed below O_{2crit} until LOE); LOE (DO at which the fish was not able to maintain a righting response); time to LOE (the amount of time between O_{2crit} and LOE). SMR was determined by removing O_2 measurements from the first 10 h (estimated chamber acclimation period) and from the hypoxia challenge using the calcSMR function in fishMO2 package (Claireaux and Chabot, 2016). The quantile method (p = 0.2) was deemed the most appropriate to calculate SMR on the remaining O_2 measurements as coefficients of variation of the mean of the lowest normal distribution (MLND) were > 5.4 in most cases (Chabot et al., 2016b). Then, after adding back the O_2 measurements from the hypoxia challenge, two functions from the R package fishMO2 were used to calculate the O_{2crit}: calcO2crit and plotO2crit (Claireaux and Chabot, 2016). The O_{2crit} was determined as the intersection of the horizontal line determining SMR and the linear regression between DO and O_2 once O_2 became proportional to DO (Nilsson et al., 2004; Claireaux and Chabot, 2016). All statistical analyses were conducted in R v.3.1.3 (R Core Team, 2014).

An index of cumulative ambient oxygen deficit ($O_{2deficit}$) (Claireaux and Chabot, 2016) integrating hypoxic severity and time was used to assess the capacity for fish to survive below O_{2crit}. $O_{2deficit}$ was determined by plotting $\dot{M}O_2$ across time and then by calculating the area between the horizontal line representing SMR and the $\dot{M}O_2$ curve between O_{2crit} and LOE (Figure 3). A pseudo-integration was conducted to calculate the area as described in (Claireaux and Chabot, 2016): $O_{2deficit} = \sum_{n=0}^{n=end}(\dot{M}O_2 - SMR) * (t_{n+1} - t_n)$.

Results were analysed using a one-way ANOVA and Tukey HSD post hoc test to identify species that significantly differ from each other. When normality and/or homoscedasticity were not verified, a Kruskal Wallis test was used in combination with a Dunn's post-hoc test. Mass was explored as a potential covariate but failed to meet the assumptions of linearity and homogeneity of variances, even after log transformation, to be included as a covariate in an ANCOVA model. Additionally, no obvious trends were observed when exploring the relationship between mass and the other metabolic measures.

5.2.4 Comparison to a field measured DO profile

To estimate the risk of exposure to hypoxia in natural mangrove environments for each species, DO measurements recorded at the Annandale Wetland, located on the Ross River in Townsville, Australia (Chapter 2), and at Bourake, New Caledonia (Chapter 4) were used to plot cumulative DO frequency curves. All four study species were observed at these two sites therefore I knew they used these areas. The average O_{2crit} values determined for each species were plotted on the cumulative DO frequency plots to estimate the percentage of time these species would have been exposed to acute hypoxia.

5.3. Results

5.3.1 Metabolic parameters

The four measured parameters selected to examine hypoxia tolerance (O_{2crit}, $O_{2deficit}$, LOE, and time to LOE) revealed significant differences among the four species (Table 6; Figure 24; one-way ANOVA: $F = 17.49$, $p < 0.0001$). *S. lineatus* had significantly lower O_{2crit}

than the three other species (Tukey HSD: $p < 0.0001$ for all significant comparisons). O_{2crit} was not significantly different among *A. pacificus*, *C. vagabundus* and *H. acuminatus*. $O_{2deficit}$ significantly varied among the four species (Figure 24; Kruskal Wallis: $\chi^2 = 20.744$, $p < 0.0005$). *S. lineatus* had a significantly greater $O_{2deficit}$ than *H. acuminatus* and *C. vagabundus* (Dunn's test: $p < 0.01$ and $p < 0.05$ respectively). Likewise, *A. pacificus* had a significantly greater $O_{2deficit}$ than *H. acuminatus* and *C. vagabundus* (Dunn's test: $p < 0.0001$ and $p < 0.0005$ respectively). No significant differences in $O_{2deficit}$ were found among the two estuarine species (*S. lineatus* and *A. pacificus*) or the two reef species (*H. acuminatus* and *C. vagabundus*; Figure 24). LOE occurred at significantly different DO values among the species (Figure 24; Kruskal Wallis: $\chi^2 = 38.493$, $p < 0.0001$). *S. lineatus* lost equilibrium at lower DO values than *A. pacificus* (Dunn's test: $p < 0.005$), *H. acuminatus* (Dunn's test: $p < 0.0001$) and *C. vagabundus* (Dunn's test: $p < 0.0001$). *A. pacificus* also lost equilibrium at lower DO values than *H. acuminatus* and *C. vagabundus* (Dunn's test: $p < 0.05$ and $p < 0.0005$ respectively). The LOE between the two reef fish species however did not significantly differ. Lastly, time to LOE also significantly differed among the four species (Figure 24; Kruskal Wallis: $\chi^2 = 18.346$, $p < 0.0001$). The time it took for *S. lineatus* to lose equilibrium was longer than *H. acuminatus* and *C. vagabundus* (Dunn's test: $p < 0.0005$ for both comparisons). Similarly, time to LOE for *A. pacificus* was significantly longer than *H. acuminatus* and *C. vagabundus* (Dunn's test: $p < 0.005$ for both comparisons). No significant differences in time to LOE were detected among the two estuarine species or the two reef species.

Table 6 Summary of metabolic measures determined for the four species tested.

Species	**n**	**Mass (g)**	**SMR ($mgO_2.kg^{-1}.min^{-1}$)**	**O_{2crit} (% saturation)**	**P_{crit} (kpa)**	**$O_{2deficit}$ ($mgO_2.kg^{-1}$)**	**LOE (% saturation)**	**Time to LOE (hh:mm)**
S. lineatus	15	96 (21-164)	1.72 (± 0.11)	13.0 (± 0.7)	2.3	85.8 (± 15.6)	7.0 (± 0.5)	02:04 (± 00:14)
A. pacificus	20	62 (21-137)	2.59 (± 0.13)	20.0 (± 0.8)	3.5	103.1 (± 11.9)	9.8 (± 0.5)	01:44 (± 00:09)

C. vagabundus	15	51 (23-71)	1.97 (± 0.11)	20.2 (± 0.7)	3.5	39.8 (± 7.0)	13.1 (± 0.6)	01:03 (± 00:07)
H. acuminatus	15	223 (155-260)	1.52 (± 0.08)	18.7 (± 0.8)	3.3	33.1 (± 4.7)	11.7 (± 0.4)	01:05 (± 00:06)

For each factor, the mean, standard error (SE), and range of values are provided when relevant.

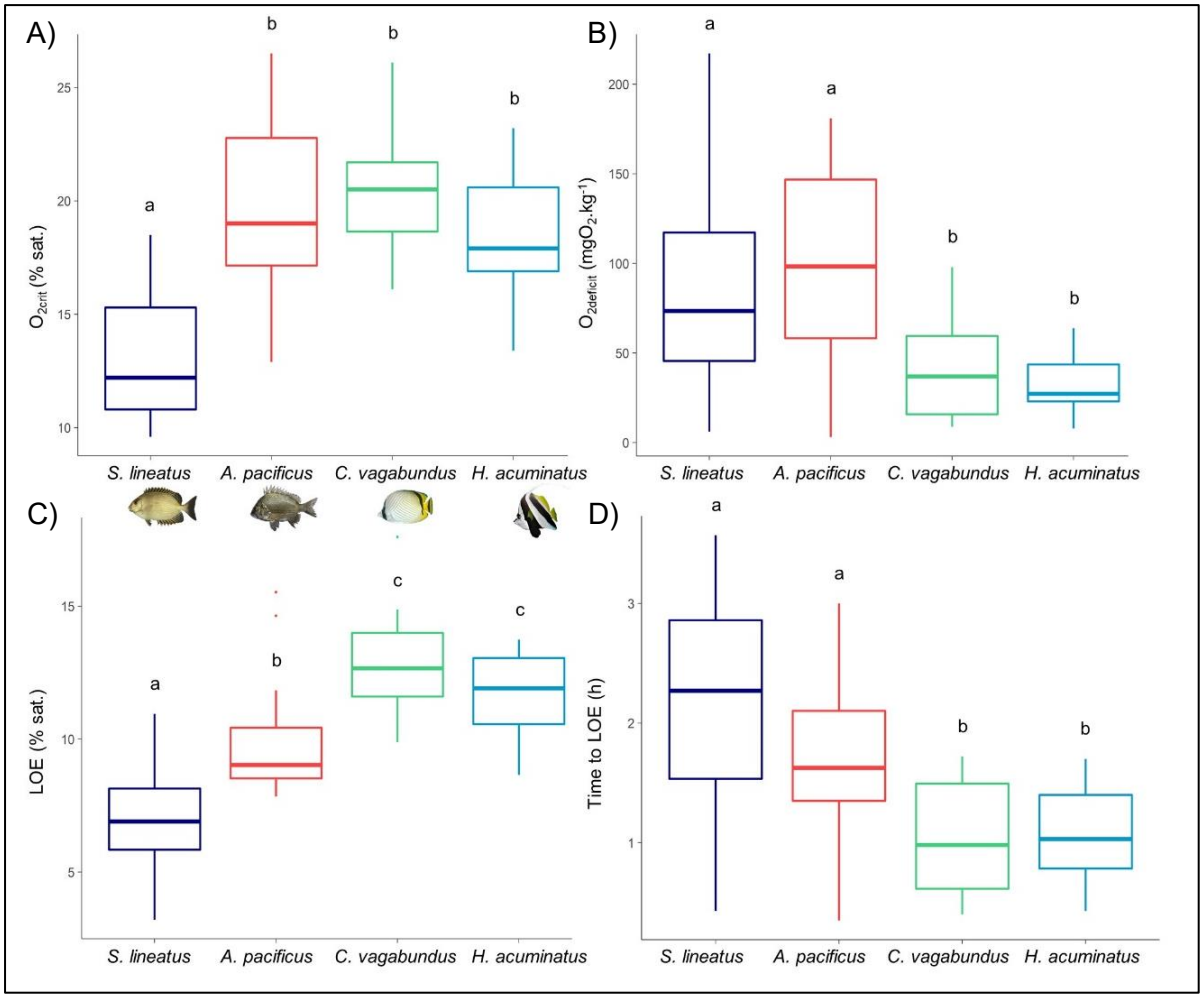


Figure 24 Variations in hypoxia tolerance among four fish species using mangrove habitats. Hypoxia tolerance is characterised by four metabolic parameters: A) O_{2crit}; B) $O_{2deficit}$; C) LOE; D) Time to LOE. Differential letters above boxes denote statistically different values between species ($p < 0.05$).

5.3.2 Risk of exposure to acute hypoxia

The O_{2crit} determined for each species was used to assess the risk of exposure to acute hypoxia in the natural environment. Cumulative DO frequencies curves obtained for the two sites where the study species were observed revealed species-specific differences in risk of hypoxia exposure (Figure 25). For 4 % of the recorded time (total of 24h over 25 days period;

Chapter 2), *A. pacificus* and *S. lineatus* would have been exposed to DO below or equal to their O_{2crit} in Annandale Wetland (Figure 25). In Bourake, *A. pacificus*, *C. vagabundus* and *H. acuminatus* would have been occasionally (total of 1h30 over 8 days period) exposed to values below or equal to their O_{2crit} (Chapter 4), while DO was never below the O_{2crit} determined for *S. lineatus* (Figure 25).

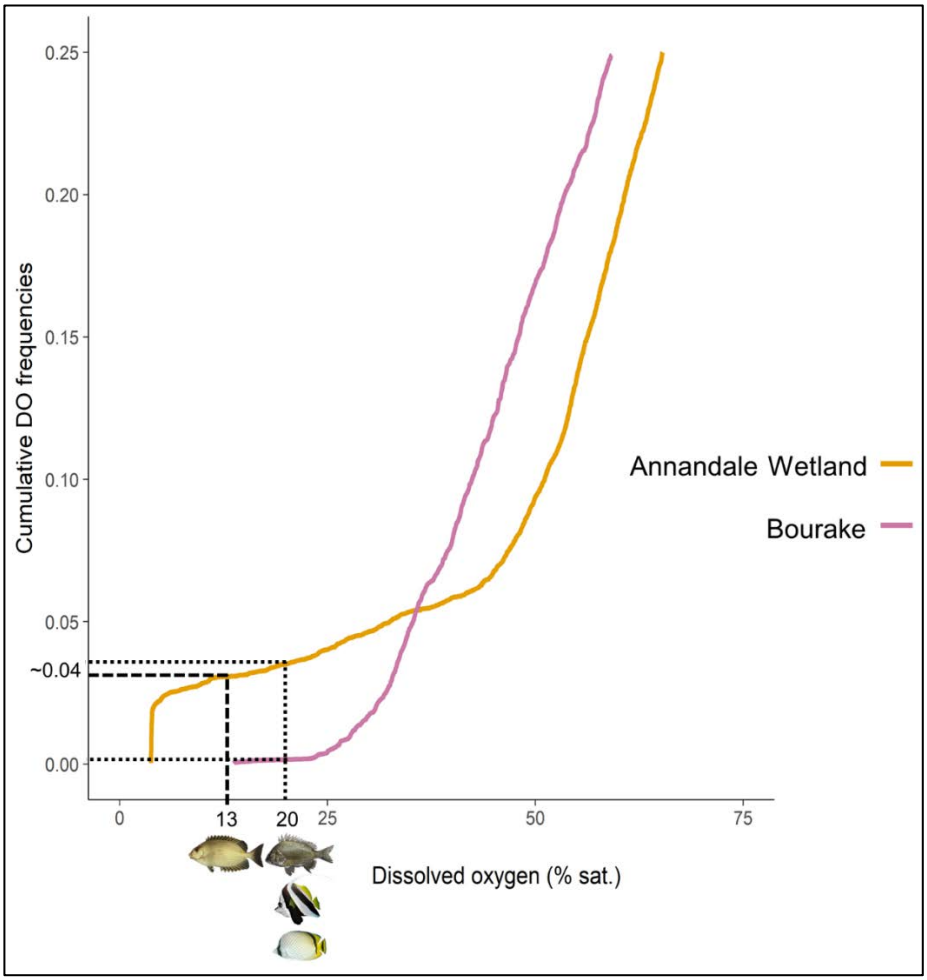


Figure 25 Risk of exposure to acute hypoxia in the natural environment for the four study species. Species-specific observed O_{2crit} are used as a threshold for acute hypoxia exposure (13 % saturation for S. lineatus and 20 % saturation for A. pacificus, H. acuminatus and C. vagabundus). The two curves represent the cumulative DO frequencies recorded for several days at two mangrove systems (Annandale Wetland, Australia and Bourake, New Caledonia) where the study species have been observed.

5.4. Discussion

5.4.1 Major findings

There is a growing need to determine thresholds to hypoxia in controlled laboratory conditions that are ecologically relevant, meaning that they approximate natural conditions and are therefore meaningful when establishing links between ecological responses and environmental hypoxia, and when evaluating the risk of exposure to hypoxia for conservation and management. Field observations of fish responses to hypoxia and laboratory studies determining metabolic performances are rarely conducted in parallel, making it challenging to infer a link between laboratory-determined thresholds and field observations. This study presents novel information combining behavioural and metabolic responses to hypoxia for four fish species known to utilise mangrove habitats that experience diel hypoxia. Field observations revealed distinct preferences for DO among the four species examined that were reflected in their metabolic responses to low DO measured via respirometry. The results from this study demonstrate that hypoxia tolerance parameters measured under controlled laboratory settings are strongly related to observed variations in occurrence of fish in mangrove habitats.

5.4.2 High tolerance to hypoxia relates to high occurrence in mangroves

The study species most commonly observed in mangrove habitats and following a "High tolerance" pattern (*S. lineatus*) was also the most tolerant to hypoxia (lowest O_{2crit} and LOE, highest $O_{2deficit}$ and longest time to LOE). Similarly, the two species that were the least frequently observed in mangroves and following a "Low tolerance" pattern (*H. acuminatus* and *C. vagabundus*) were the least tolerant to hypoxia (highest O_{2crit} and LOE, lowest $O_{2deficit}$ and shortest time to LOE). *A. pacificus* was almost as commonly observed in mangrove habitats as *S. lineatus*, but was following a "Medium tolerance" pattern. This species was more tolerant to hypoxia than the two reef fish species (lower LOE, highest $O_{2deficit}$ and longer time to LOE) but less tolerant than *S. lineatus* (higher O_{2crit}). These results indicate that fish species which are more highly associated with mangrove habitats may also have a correspondingly high tolerance to hypoxia. While the O_{2crit} of *A. pacificus* was similar to *C. vagabundus* and *H. acuminatus*, this species displayed better hypoxia tolerance at DO below O_{2crit}. Such higher

resistance to hypoxia may allow *A. pacificus* to use mangrove habitats more effectively than the two reef species. Interestingly, *C. vagabundus* and *H. acuminatus* showed similar patterns of utilisation (both entirely absent at DO < 70 % saturation) that were associated with similar and poorer ability to tolerate hypoxia than the two estuarine species. A previous study, combined field observations in intertidal rockpools in New Zealand where the team studied two fish species distributions and their metabolic measurements. The authors identified that the species having the highest tolerance to hypoxia was able to inhabit warm and hypoxic rockpools while the other species was missing, thus suggesting that species tolerances to hypoxia was an important factor to explain habitat utilisation (Hilton et al., 2008).

5.4.3 Mangrove-associated species have a better ability to maintain aerobic metabolism

S. lineatus displayed the lowest O_{2crit} in this study, that also occurred to be lower than observed O_{2crit} of fish species primarily associated with coral reefs (O_{2crit} = 13-34 % saturation) (Nilsson and Ostlund-Nilsson, 2004; Wong et al., 2018) and other fish associated with mangrove habitats in tropical Australia (e.g. barramundi; 16-20 % saturation (Collins et al., 2013). Juveniles *S. lineatus* are commonly found in mangrove habitats that naturally experience lower DO levels (Chapter 4; Sheaves et al., 2016) than coral reef habitats (Camp et al., 2017; Wong et al., 2018). Fish frequently and repetitively exposed to hypoxia have developed strategies to tolerate and exploit these hypoxic environments. The lower O_{2crit} measured in *S. lineatus* indicates a higher capacity for oxygen extraction and tissue delivery at low DO (Mandic et al., 2009), and suggests that *S. lineatus* is better adapted to use mangrove habitats, allowing it to thrive in these hypoxic environments, compared to fish that are more frequently associated with adjacent reef habitats.

5.4.4 Mangrove-associated species have a better capacity to survive below O_{2crit}

Capacity to survive below O_{2crit} is critical to resist to hypoxia. *S. lineatus* and *A. pacificus* had a better capacity to survive below O_{2crit} (higher $O_{2deficit}$) compared to *C. vagabundus* and *H. acuminatus*. These results suggest that species commonly using mangrove habitats may also be better adapted than reef-associated species to resist to hypoxia when DO levels fall below their O_{2crit}. The utilisation of anaerobic pathways and the capacity to perform metabolic rate depression predict survival below O_{2crit} (Richards, 2009). Therefore, it is probable that *S. lineatus* and *A. pacificus* are better adapted to perform anaerobiosis and metabolic rate depression compared to the two reef fish species. This may explain why they were remaining in mangrove habitats at DO levels closer to their O_{2crit}, whereas the two reef fish species were avoiding the area at DO much above their O_{2crit}. The high inter-individual variability for time to LOE, and consequently for $O_{2deficit}$, observed for both mangrove-associated species (> 4-fold for both measurements) may however highlight that the capacity to survive below O_{2crit} varies between individuals and could be the result of different genetic pools or different life-histories exposure to hypoxia (Vanderplancke et al., 2015; Norin et al., 2016). Based on the results from chapter 4 that highlighted 3 main patterns of mangrove utilisation across DO for 36 common fish taxa, I hypothesise that the results found in chapter 5 for 4 model species would be applicable to the other 32 species. Thus, taxa following a “High tolerance” pattern will have a greater hypoxia tolerance than taxa following a “Medium tolerance” pattern that would themselves have a greater hypoxia tolerance than taxa following a “Low tolerance” pattern.

5.4.5 Acute hypoxia thresholds do not predict behavioural avoidance

The four parameters assessed via respirometry established that the ability to tolerate hypoxia (capacity to maintain aerobic metabolism and capacity to survive below O_{2crit}) was related to mangrove habitat utilisation for the species examined in this study. However, all species displayed avoidance strategies at DO levels substantially higher than their O_{2crit} in the environment, except *S. lineatus* that did not display avoidance within the range of DO values recorded. Fish respond to DO levels well above O_{2crit} because they rapidly start suffering from

a shortage in oxygen as DO falls under saturation, compromising other physiological functions (Richards, 2009). Indeed, fish in the environment engage in many physiological functions, usually supressed during experiments, such as digestion, swimming, foraging and avoiding predators. These activities increase the metabolic demand above SMR and concurrently diminish the metabolic scope available to respond to hypoxia (Wang et al., 2009; Jourdan-Pineau et al., 2010; Zambonino-Infante et al., 2017). Additionally, when environmental hypoxia occurs, it is usually accompanied by other stressors such as high temperature, low pH, or high concentration of toxins that can reduce hypoxia tolerance (Sokolova, 2013), and consequently lead to fish responding to environmental hypoxia much before it reaches their acute hypoxia tolerance threshold.

A good indicator to determine when fish are likely to start responding to environmental hypoxia is the DO level at which haemoglobin saturation in oxygen starts to decrease, indicating the potential to limit aerobic activities and consequently to lead to sublethal effects (Richards, 2009; Rummer and Brauner, 2015). Sublethal effect thresholds may better relate to behavioural avoidance and could predict the differential DO preferences observed in the field for the four study species. For instance, the two reef fish species avoided mangrove habitats at 70-80 % saturation, that interestingly is often used by physiologists as a threshold for normoxia because majority of studies have highlighted a sharp decline in haemoglobin-O_2 binding affinity at these levels (Rummer et al., 2013; Svendsen et al., 2016). To minimise the concomitant reduction in aerobic scope that is associated with declining DO, it is very likely that fish start displaying behavioural avoidance at sublethal hypoxia thresholds and not at acute hypoxia thresholds.

Metabolic parameters measured in this study provide useful information on ecological responses to hypoxia. However, such measures do not fully represent the species overall hypoxia tolerance (Claireaux and Chabot, 2016; Wood, 2018; Regan et al., 2019). Indeed, this study strongly suggests that fish species responded to DO levels substantially higher than their acute hypoxia tolerance threshold, meaning that species relocation, and therefore critical changes in ecosystem functioning, may happen much before O_{2crit} is reached. Therefore,

caution should be exercised in the application of O_{2crit} as a conservative hypoxia threshold in natural environments because it most likely underestimates the impact of environmental hypoxia. The ecological relevance of O_{2crit} is most of the time overlooked and not validated as laboratory studies determining hypoxia tolerance thresholds are mostly conducted without field data to support their findings. To increase the applicability of O_{2crit}, additional information can be collected by measuring the total hypoxia response (Mandic and Regan, 2018), and by characterising sublethal effects such as increase ventilation rate, avoidance behaviour and haemoglobin-O_2 binding affinity (Mandic and Regan, 2018; Wood, 2018; Regan et al., 2019). These measures need to be determined in experimental conditions that are ecologically relevant and standardised when applicable (for instance units or calculations/determinations; (Wood, 2018; Regan et al., 2019). Subsequently, it is essential to understand the implications of the laboratory findings and validate their applicability in the natural environment.

5.4.6 Ecological implications of this study

Natural diel-cycling hypoxia temporarily reduces habitat value of mangroves and likely shapes mangrove fish assemblages. Field measurements conducted in habitats commonly used by the four study species showed that, on most days, DO reached values below their O_{2crit}. Below this threshold, short-term survival is compromised, and additionally, fish may suffer from sublethal effects much before O_{2crit} is reached. Minimum DO values recorded (13 % saturation in Bourake, Chapter 4; and near-zero saturation in Annandale, Chapter 2) were even below their 'near-death' (LOE) thresholds and would lead to mass mortalities if fish remain. It is expected that the results found for these 4 species apply to most species found in mangrove habitats. Therefore, this study suggests that DO impacts the mangrove fish community by favouring highly tolerant species and by temporarily or permanently excluding sensitive species. Species not specifically adapted to deal with low DO are probably not venturing in mangrove habitats. The concept that increased hypoxia tolerance confers a greater capacity to utilise mangrove habitats may explain the relatively low fish diversity found in some intertidal mangrove habitats, with few species usually dominant in the community (Lal,

1984; Quinn and Kojis, 1985; Blaber et al., 1989; Robertson and Duke, 1990; Thollot, 1992; Castellanos-Galindo et al., 2012; Reis-Filho et al., 2016; Sheaves et al., 2016). It can also help to explain the lower contribution of coral reef fish species to mangrove fish assemblages in highly-dynamic intertidal mangrove habitats compare to the Caribbean that could experience higher and stable oxygen conditions (Chapter 2; Chapter 4; Lal, 1984; Quinn and Kojis, 1985; Thollot, 1992; Laroche et al., 1997; Mumby et al., 2004; Dorenbosch et al., 2007; Unsworth et al., 2009; Barnes et al., 2012).

5.5. Conclusion

There is abundant evidence that hypoxia is increasing in coastal habitats and it is considered as one of the most pressing threats to the ocean (Breitburg et al., 2018). Coastal habitats such as mangroves are prone to natural occurrences of hypoxia (Chapter 2; Chapter 4; Mattone and Sheaves, 2017) and anthropogenic disturbances, such as agriculture, urbanisation (Pollock et al., 2007) and climate change (Keeling et al., 2009) are likely to exacerbate this natural phenomenon. If severity and occurrence of hypoxia in mangrove habitats were to increase, it could have disastrous consequences for mangrove ecosystems functioning. This study has shown that fish species using mangrove habitats are highly tolerant to hypoxia, however it also showed that these species are already dealing with DO conditions approaching their physiological limitations, therefore, if further degraded, hypoxia could cause loss of mangrove habitats value and have severe consequences for fish communities.

5.6. Summary

To test whether differential hypoxia tolerances could explain mangrove habitats utilisation patterns revealed in chapter 4, laboratory experiments were conducted on 4 species displaying different patterns in response to DO. Results showed that the most hypoxia tolerant species (*Siganus lineatus*) was not displaying any apparent DO avoidance, accessing mangrove habitats even at low DO, while the least tolerant species (*Heniochus acuminatus* and *Chaetodon vagabundus*) were avoiding mangrove habitats at DO below 70-80 %

saturation. These findings suggest that mangrove utilisation relates to species hypoxia tolerance in terms of both DO preferences and occurrence, supporting the hypothesis that hypoxia may be a pre-condition for fish to thrive in mangroves. The resulting selectivity for highly tolerant species could explain the low taxonomic richness recorded in other intertidal mangrove habitats, or their low utilisation by reef fish species that are not known to naturally use hypoxic habitats.

Chapter 6 General discussion

6.1. Ecological implications

6.1.1 General use of intertidal mangrove habitats

Mangrove habitats are commonly viewed as important nursery, refuge and feeding grounds for fish (Nagelkerken et al., 2008). However, the reality is much more nuanced, with their relative importance determined by location-specific characteristics such as their geographical location, setting (estuarine, coastal, marine), connectivity with other habitats, tidal range (micro-, meso- or macrotidal), and tidal cycle (semi-diurnal, diurnal, mixed tides) (Bradley et al., 2019).

Chapter 3 provides a detailed investigation of the use of an intertidal mangrove forest nearby coral reefs located in a microtidal area of the Indo-West Pacific. The results did not support the hypothesis that mangrove habitats act as important nursery, refuge or feeding grounds, actually showing that overall fish make a very limited use of these habitats, and that fish using them extensively are highly adapted to do so. Relatively few species were recorded in the study area compared to adjacent coral reef habitats, suggesting that the use of intertidal mangrove habitats is limited. Few feeding activities were recorded, conducted by a small portion of taxa, consisting mostly of bottom feeders such as *Gerres oyena, Parupeneus indicus*, Mugilidae spp., and Gobiidae spp., or grazers like *Siganus lineatus, Chaetodon auriga, Acanthurus auranticavus, and Scarus* sp. However, in-situ observations of predator-prey interactions are rare, therefore, feeding activities were probably underestimated. For instance, *Lutjanus argentimaculatus*, *Acanthopagrus* spp., and *Epinephelus* spp., are known to specifically feed on mangrove-associated sesarmid crabs (Sheaves and Molony, 2000). Except for these specific taxa, studies have shown contrasting results concerning food availability in mangrove habitats, and therefore questioned their value as feeding grounds. For example, (Mattone, 2016) has not recorded any peracarids inside mangrove forests in north-east Australia, that represent a key prey source for many fish taxa. Similarly, the extensive

use of prop-root structures as shelter (Laegdsgaard and Johnson, 2001; Nagelkerken and Faunce, 2008) was questioned here as fish were mostly observed cruising on the edge of the forest with few individuals actively sheltering among mangrove prop-roots. The mangrove forest studied provided no evidence that predation was on average reduced, as has been suggested in numerous studies (Nagelkerken et al., 2008). Predatory fish were observed, visibility was good, and on the edge of the forest water depth was deep enough to allow access to large fish. This was even confirmed by the observation of several large bull sharks hunting along the mangrove edge. These results suggest that the role of mangrove forests as refuges may be limited, with fish mostly cruising along the edge and potentially using the forest as a refuge when feeling threatened. A total of 12 juvenile species were recorded, also highlighting the limited importance of intertidal mangrove habitats as nursery grounds.

The findings of this thesis only fuel the debate around the value of mangrove habitats for fish. The general assumptions that mangrove habitats globally act as important nurseries, feeding grounds or shelters need to be reconsidered and explored case by case. The role mangrove habitats play is clearly defined at the whole ecosystem-scale and depends on local characteristics, and consequently vary within locations (Sheaves, 2005; Bradley et al., 2019). Moreover, different values are most likely associated with different components of mangrove habitats such as the edge of the forest and the in-forest, leading to high spatial variations in fish assemblages among studies.

6.1.2 Risks of stranding and hypoxia limit the use of mangrove habitats

6.1.2.a Permanent limitations

Tidal fluctuations are a permanent constraint for fish using intertidal habitats as they are responsible for rapid and extreme physical and chemical changes that can drastically reduce habitats value (Furukawa et al., 1997; Krumme et al., 2012) and justify for their limited use. Because the numerous changes driven by tides can be discrete, synergistic or antagonistic, it is difficult to quantify their specific influence on fish assemblages, and as a result, their relative importance is often not fully understood. This study is the first to investigate

the role of two key limiting factors, depth and DO, in controlling fish utilisation of a tropical intertidal mangrove forest.

Results from chapter 3 and 4 suggest that the combined risks of stranding and hypoxia that species face constantly, induced by rapid and sharp declines in depth and DO, can partly explains the low species richness generally recorded in intertidal mangrove habitats (Laroche et al., 1997; Barnes et al., 2012; Reis-Filho et al., 2016; Sheaves et al., 2016). Indeed, these harsh conditions imply that fish need specific adaptations to deal with intermittent availability and suitability of mangrove habitats. Increasing risks of stranding and hypoxia with distance inside the mangrove forest (Mattone and Sheaves, 2017) also probably prevent species from venturing deep inside mangrove forests. Instead, most species were rather observed cruising on the edge, especially at deeper sites that remain available throughout the entire tidal cycle and provide more stable environmental conditions. The edge may provide opportunistic feeding and allow fish to retreat inside the forest if endangered, but also provide an easy escape route from falling water depth or developing hypoxic conditions. Therefore, using the mangrove fringe seems to offer a good compromise for fish to enjoy the benefits of mangrove habitats while limiting the hazards related to the use of these intertidal habitats. These results corroborate those of another study conducted in intertidal mangrove forests of north-east Australia (Sheaves et al., 2016), suggesting that these patterns of utilisation could be a widespread feature among intertidal mangrove forests.

6.1.2.b Temporary limitations

Tidal fluctuations probably exclude permanently a substantial amount of species, but chapter 3 also reveals that tidal fluctuations temporarily exclude fish using mangrove habitats in a species-specific way. Species not recorded in the area below a certain depth threshold most likely highlight that these species resort to tidal migrations to avoid unfavourable conditions. Fish tidal migrations are often recorded in intertidal environments, usually initiated as an active process in response to changing environmental conditions (Burrows, 2001; Rountree and Able, 2007; Ellis and Bell, 2008; Reis-Filho et al., 2016). Fish can use tidal

migrations to maximise the benefits of utilising intertidal zones, and escape to more suitable adjacent habitats when intertidal habitats become either inaccessible or unsuitable (Barletta et al., 2000; Rountree and Able, 2007; Ellis and Bell, 2008). Tidal migrations are adopted as an advantageous strategy by many species (Ellis and Bell, 2008), however, they also have inconveniences. First, fish need to have access to cues to determine when and where they need to migrate before being exposed to danger (Chabot and Claireaux, 2008; Ellis and Bell, 2008). Second, suitable adjacent habitats need to be accessible within a few meters as it is unlikely that fish will engage in long migrations over a tidal-scale (Tulevech and Recksiek, 1994; Krumme, 2009). Third, performing tidal migrations require energy that is therefore not directed towards other activities such as growth, reproduction, or feeding, potentially reducing fitness (Gibson, 2003). Fourth, tidal migrations can aggregate fish in suboptimal habitats, increase their predation risk, decrease their feeding opportunities, or make them more vulnerable to fishing gears (Gibson, 2003). Consequently, fish undertaking tidal migrations have evolved to maximise the benefits and limit the costs (Krumme, 2009) associated with this strategy. Thus, these results corroborate the idea that only adapted species capable of undertaking tidal migrations use intertidal mangrove habitats, representing a strong selective factor shaping mangrove fish assemblages. However, if species have evolved to be specifically adapted to use intertidal mangrove habitats, this probably emphasises the importance of their value for these species.

Triggers responsible for initiating tidal migrations in fish remain unclear, but chapter 3 and 4 suggest that fish could respond to both falling depth and DO. As depth decreases, fish can use the receptors on their lateral line, that are sensitive to changes in hydrostatic pressure, (Mogdans and Bleckmann, 2012; Liu et al., 2016) to move away before risk of stranding becomes too high. Although depth seems to be the most obvious factor to explain tidal migrations, chapter 2 and 4 have shown that depth and DO are highly collinear. Depth becomes limiting once fish cannot longer safely access the area, while DO becomes rapidly limiting below saturation as it impairs physiological processes (Chabot and Claireaux, 2008; Vaquer-Sunyer and Duarte, 2008). This suggests that most of the time hypoxia could actually

represent a greater risk than stranding, and as a consequence, be the main trigger of fish tidal migrations. Few studies have suggested that fish can directly sense DO, allowing them to orientate towards more oxygenated areas (Wannamaker and Rice, 2000). This process may be explained by the presence of a molecular sensor to oxygen (Wu, 2002) that would allow fish to use ambient DO as a cue to initiate tidal migrations. However, fish could also benefit from the high collinearity between depth and DO and use depth as a proxy for upcoming hypoxia, therefore seemingly responding to depth but in fact avoiding hypoxia. For instance, Brady and Targett (2013) looked at fish migrations in response to DO and found that juvenile weakfish and spot were using ebb tidal flow to escape low DO, potentially responding to current or changes in hydrostatic pressure. The confounded effects of depth and DO are extremely difficult to disentangle, and this is because fish probably use depth and DO interchangeably as cues to initiate tidal migrations depending on which factor becomes limiting first (stranding or hypoxia). These cues could for instance change in a species-specific way depending on tidal direction, as flooding tides could potentially allow DO to replenish quicker than depth, while ebbing tides would carry hypoxic water from sediments and in-forest, reducing DO faster than depth.

6.1.3 Hypoxia tolerance could explain mangrove utilisation

DO is a factor rarely considered when investigating the value and utilisation of mangrove habitats, with only three studies prior to this thesis that have looked at detailed short-time scale DO fluctuations (Knight et al., 2013; Gedan et al., 2017; Mattone and Sheaves, 2017). Similarly to these studies, the two different locations I sampled in chapter 2 and chapter 4 experience diel hypoxia, reaching levels that had been linked to physiological and behavioural responses of fish, and even death in the literature (Rogers et al., 2016). These two locations were in the Indo-West Pacific, in areas experiencing moderate and high tidal amplitudes. Tidal factors were shown to largely contribute to DO declines that coincided with ebbing tides for both locations, probably explained mostly by the tidal-pumping theory (Maher et al., 2013; Call et al., 2015). These results highlight that hypoxia is likely to be a widespread

environmental condition in intertidal mangrove habitats and consequently should be considered as a strong selective factor in determining fish communities as it has been demonstrated to be in other hypoxic environments (Hilton et al., 2008; Mandic et al., 2009; Chapman, 2015; Gallo et al., 2019), but for some reasons has been overlooked in mangrove habitats.

The combination of field data (chapter 4) and laboratory analyses (chapter 5) allowed to establish that in-situ species-specific responses to declining DO relate to differential tolerances to hypoxia. Even if further analyses are necessary to confirm this trend, species frequently observed, including at low DO levels, such as *Siganus lineatus* and *Acanthopagrus pacificus*, were shown to have a higher capacity to extract and transport oxygen and to perform in anaerobiosis compared to less frequently observed reef-associated species avoiding DO levels below 70-80 % saturation such as *Heniochus acuminatus* and *Chaetodon vagabundus*. Mangrove-associated species likely rely on physiological adaptations that they have developed over time after frequent exposures to hypoxia making them more tolerant (Borowiec et al., 2015) and allowing them to thrive in these temporarily hypoxic environments.

High tolerance to hypoxia may be a required pre-condition to extensively use intertidal mangrove habitats and would therefore act as a strong selective factor and partly explain why mangrove fish species richness is usually limited with only few taxa dominating the assemblages (Robertson and Duke, 1990; Dorenbosch et al., 2005; Reis-Filho et al., 2016; Sheaves et al., 2016). Mangrove fish assemblages in regions with a small tidal amplitude such as the Caribbean tend to comprise not only mangrove-associated species but also reef-associated species (Nagelkerken et al., 2000a; Nagelkerken et al., 2001; Mumby et al., 2004; Dorenbosch et al., 2007), that are usually absent or limited in regions with a higher tidal amplitude, even in mangrove habitats located nearby coral reefs (Lal, 1984; Quinn and Kojis, 1985; Thollot, 1992; Laroche et al., 1997; Unsworth et al., 2008; Barnes et al., 2012). These discrepancies could possibly be explained by DO, as in the absence of tide, mangrove habitats could experience higher and more stable DO than intertidal forests, providing more favourable environmental conditions for reef fish species. Indeed, as coral reef species are not known to

naturally experience diel hypoxia, they would not be adapted to deal with DO levels recorded in intertidal mangrove habitats and consequently would not use them because of a high risk of physiological impairment. However, no studies have investigated DO dynamics in clear-water coastal mangrove habitats subjected to small tidal amplitudes such as in the Caribbean. Evaluation of these dynamics in future studies will assist in determining whether hypoxia conditions also occur in non-intertidal coastal mangrove habitats and confirm whether DO conditions can help to explain discrepancies in fish communities between locations experiencing high and small tidal amplitudes.

Surprisingly, most of the recorded time DO levels were above the determined acute hypoxia tolerance thresholds of the two study reef fish species (chapter 5), and were similar to the thresholds of reef fish species determined by other study (Nilsson and Ostlund-Nilsson, 2004; Wong et al., 2018). These thresholds indicate that, similarly to mangrove-associated species, reef fish species could use mangrove habitats even at the lowest DO values recorded (up to 30 % saturation) without being exposed to lethal values. However, most reef fish species were displaying apparent behavioural avoidance at 70-80 % saturation, much before their acute hypoxia tolerance thresholds, while mangrove-associated species were recorded at DO levels closer to their acute hypoxia tolerance thresholds. This behavioural response threshold is an interesting result as 70-80 % saturation is often used by physiologists as the limit for normoxia during experiments (Svendsen et al., 2015) because a sharp decline in haemoglobin O_2 saturation is usually observed around these values (Rummer et al., 2013) and lead to sublethal effects such as reductions in growth or reproduction (Wu, 2002; Chabot and Claireaux, 2008). Perhaps species commonly using mangrove habitats are also better adapted to mitigate sublethal effects, while coral reef species may rapidly experience sublethal effects. These results highlight that acute hypoxia tolerance thresholds do not fully represent species overall hypoxia tolerance and therefore do not predict behavioural avoidance. Determining sublethal effects following diel-cycling hypoxia exposure is a future research direction that would allow for a more complete understanding of the impact of hypoxia on

mangrove fish assemblages and would be very informative for management and conservation purposes.

6.2. Management and conservation implications

6.2.1 Local management considerations

Mangrove habitats are facing numerous anthropogenic threats, mostly generated by agriculture, coastal development, and increasingly urbanisation, compromising their value and utilisation (Kathiresan and Bingham, 2001; Alongi, 2002; Sheaves et al., 2014). These threats can modify hydrological flows, alter water quality, impede biological connectivity, and have severe consequences on mangrove functioning (Sheaves et al., 2014). In response to the intensification of anthropogenic degradation, projects aiming to increase mangrove habitats protection, replant mangrove trees to offset the loss of others, and rehabilitate degraded mangrove habitats have flourished in the recent years globally (Lewis and Gilmore, 2007; Dale et al., 2014; Das, 2017). A comprehensive knowledge base on mangroves functioning is important to maximise the probability of success of these projects (Sheaves et al., 2014). However, much about mangroves functioning is still not fully understood, and there is a need for more specific research to truly understand the function and importance of mangrove habitats to better inform managers and policy makers (Lee et al., 2014; Sheaves et al., 2014; Sheaves et al., 2016). This thesis illustrates well this lack of knowledge, as it is the first study to investigate the role of a crucial limiting factor, oxygen, in affecting fish assemblages, despite that mangroves have been known to be hypoxic environments.

This thesis provides important information for management as it shows that there is a high spatial and temporal variability in mangrove utilisation induced by tidal and diel variations of abiotic factors such as depth, DO, lunar phase, mangrove components habitats, time of day and tide direction. This implies that depending on when and where sampling is conducted, results obtained to characterise the importance of a site can be substantially different and lead to inaccurate, flawed and unsubstantiated conclusions if the sampling is not conducted appropriately or generalised from one location to another. Consequently, high variability

among and within locations provides challenges for ecosystem managers because it cannot be assumed that mangrove habitats are all equivalent and require the same conservation and restoration strategies. Previous studies such as (Beck et al., 2001; Igulu et al., 2014; Sheaves et al., 2016; Sheaves, 2017; Bradley et al., 2019), supported by the current one, advocate for an approach that takes management decisions at site-specific level, supported by a robust understanding of context (Bradley et al., 2019), and local data on abiotic factors collected at an appropriate temporal and spatial scale. For instance, local data need to be collected over several days and tidal cycles, at different time of day and at multiple spots within a same location to accurately capture variability within the system. Accounting for these factors while assessing the value of mangrove habitats would surely lead to an overall better implementation of management decisions.

Budgets and timeframe are often limited, therefore, prioritising management actions and assuring their success is crucial. However, unsuccessful mangrove rehabilitation projects are frequently reported (Lewis and Gilmore, 2007; Bosire et al., 2008; Mangora, 2011), due to a lack of basic understanding about mangrove functioning (Dale et al., 2014). For instance, water quality is rarely considered or monitored before, during, and after rehabilitating mangrove habitats. However, water quality is crucial and often compromised by former actions, or restoration actions such as digging, installation of small and large-scale barriers, water pumping, nutrient-enriched water sewage, and aquaculture ponds. For instance, low DO and acid sulfate soils are common stressors occurring after digging actions are conducted to modify tidal connectivity or hydrology (Chapter 2; Sammut et al., 1996; Lin et al., 2004; Alsemgeest et al., 2005). If water conditions are toxic for the fauna, no life will return even if connectivity is restored. Therefore, if suitable water quality, especially DO, pH, temperature, and sulfuric acid, as well as connectivity to other important habitats such as seagrass, rocky and coral reefs, or any other structured habitats are assured (Lefcheck et al., 2019), more successful projects will be carried on.

Managers also need to be able to distinguish from anthropogenic and natural changes occurring in mangrove habitats. Mangroves are dynamic and complex environments, often

presenting extreme conditions. However, many species are adapted and will take advantage of these naturally non-optimal conditions over less tolerant species to thrive. For instance, this thesis has shown that diel hypoxia naturally occurs in mangrove habitats and species are specially adapted to deal with this stressor. Therefore, normoxia is not the only valid reference condition when assessing the water quality of mangrove habitats. However, if human-induced changes amplify these natural extreme conditions, this could have disastrous consequences and would need to be addressed.

This study has revealed that mangrove habitats can be temporarily unsuitable, thus many species will only use them transiently, undertaking tidal migrations to adjacent habitats on which they also depend. It has also established that few species physically use intertidal mangrove habitats, suggesting that their importance in sustaining fish populations is more complex than previously thought (Sheaves et al., 2016). Direct utilisation of mangrove habitats may benefit few species, however, it is likely that they indirectly sustain fish populations by for instance transferring organic matter to adjacent habitats through faunal migrations and tidal connections (Sheaves and Molony, 2000; Sheaves, 2005; Francis and Côté, 2018). This study supports the idea that the importance of mangrove habitats for fish populations needs to be considered at an ecosystem scale, with mangrove habitats being one of the essential habitats forming a mosaic of interconnected habitats (Nagelkerken et al., 2013; Sheaves et al., 2016). Consequently, it is important to consider a whole-ecosystem approach to management and restoration (Sheaves et al., 2014), that have proved to be successful in temperate estuaries (Weinstein et al., 2005; Weinstein and Litvin, 2016). Adopting this approach would surely improve our ability to locally protect, conserve and restore tropical mangrove habitats and consequently entire ecosystems functioning.

6.2.2 International management considerations

Pressures on the ocean are increasing worldwide. One of the most prominent issues is the global loss of oxygen, referred to as ocean deoxygenation (Diaz and Rosenberg, 2008; Breitburg et al., 2018). Discharge of nutrients including nitrogen, phosphorus and organic

matter to the ocean, as well as climate change, are the two primary causes of ocean deoxygenation (Breitburg et al., 2018). Mangrove habitats are particularly vulnerable as they are located along the coasts, strongly influenced by their watershed directly receiving nutrient-enriched effluents. The evidence that mangrove habitats already experience natural diel hypoxia, is concerning for the future. As this study has shown, some species inhabiting mangrove habitats temporarily or permanently live on the edge of oxygen limitation. Consequently, further degradation of DO conditions by human-caused changes may lead to the complete exclusion of species, resulting in the loss of mangroves as valuable fish habitats.

There is no easy solution against ocean deoxygenation. However, ocean deoxygenation needs to be considered as one of the most important aquatic stressors, with the main causes addressed if we are to stop the spread of ocean deoxygenation and prevent the loss of key habitats such as mangroves. International management actions need to be taken to reduce nutrient and organic matter enrichment as well as greenhouse gas emissions (Conley et al., 2009; Breitburg et al., 2018). Improving understanding of the extent of ocean deoxygenation and the consequences on mangrove systems is also crucial to predict and offset future impacts. Many questions remain that adequate monitoring at appropriate temporal- and spatial-scale can address (Breitburg et al., 2018). Accurate monitoring can help understanding, detecting and predicting hypoxic events and limit mass mortality events or disruption of mangrove functioning in the long term and therefore monitoring programs should be implemented more broadly and data made available to track and manage human-induced changes in mangroves. The improvement of water quality monitoring technologies has provided crucial tools to managers, scientists and policy makers to monitor and record DO fluctuations and its effects, and to model and predict hypoxia occurrence. However, continued local and regional DO monitoring data are still limited and rarely used to design laboratory experiments or develop modelling tools, reducing our ability to predict the effects of hypoxia, changes in DO dynamics and outcome of management action plans and policies at local, regional and global scales.

Most guidelines specify that management actions are necessary if DO falls below 2 $mg.L^{-1}$, representing a commonly used hypoxia threshold (Pihl et al., 1991; Diaz, 2001; Breitburg et al., 2018). However, the adoption of this value as a conventionally accepted hypoxia threshold is misleading when used for management and conservation purposes. Indeed, studies have shown that many species respond to falling DO prior to this threshold (Vaquer-Sunyer and Duarte, 2008), and this has also been observed during this study. Therefore, 2 $mg.L^{-1}$ is not conservative enough if we are to protect the majority of species, including the most sensitive ones. Moreover, hypoxia rarely occurs as the only stressor, but is usually associated with low pH, high temperatures, and presence of toxins such as sulphates, ammonia and methane, that can reduce hypoxia tolerance (Wu, 2002; Breitburg et al., 2018). Therefore, guidelines need to be conservative enough to allow for cumulative adverse effects. On the other hand, numerous species are highly adapted to hypoxia, and thrive in environments commonly experiencing DO levels below 2 $mg.L^{-1}$ (Mandic et al., 2009; Fagernes et al., 2017; Gallo et al., 2019), including mangrove habitats (Chapter 4; Chapter 5). Concluding that these habitats cannot support aquatic life because DO levels are too low, and consequently need to be restored or disregarded as important habitats is inappropriate. High variability in hypoxia tolerance thresholds, and therefore, in the associated effects on marine ecosystems, emphasise that adopting one single universal hypoxia threshold is not realistic. A better approach is to consider taxon-specific thresholds to allow the implementation of more specific guidelines and conservation strategies, as well as the development of models capable of predicting distribution of, and changes in fish populations in response to hypoxia.

6.3. Thesis limitations and future directions

This thesis provides important knowledge about the impact of diel hypoxia on the value of mangroves as fish habitats. However, this thesis only investigated one location to quantify the effect of DO on fish utilisation and therefore more studies would be needed to assess if these results apply to other locations. Future studies should focus on other geographical locations experiencing different tidal ranges as tide was shown to be largely responsible for

DO fluctuations. Different settings should also be tested, especially estuarine settings, as it is expected that estuarine mangrove habitats would experience lower DO than coastal mangrove habitats, resulting in lower species richness dominated primarily by species highly tolerant to hypoxia.

The underwater video camera (UVC) technique was used during this study. While this technique has many advantages, it also carries limitations. UVCs can only be used during daytime, therefore, this study does not provide any information about fish assemblages at night. The relationship between DO and fish utilisation could be different and even more pronounced as lowest DO levels were usually recorded at night, reaching lethal levels, therefore, night sampling would be highly informative. Results obtained with UVCs were based on the presence or absence of fish, therefore no information was available about where missing fish were. Future studies could use acoustic tagging techniques to specifically track fish movements and identify adjacent habitats that fish use when leaving mangrove habitats. This technique will also enable the exclusion of the hypothesis that some fish species were not recorded on the UVCs because they were at the surface using the first few centimetres of highly oxygenated water, out of the field of view of the camera. While this behavioural technique cannot be performed by all species, adapted species may resort to surface respiration and air-gulping when conditions worsen.

During this thesis, I have collected data only during summer as it is the season that poses more problem for hypoxia because of high water temperature. Mangrove habitats utilisation could be substantially different during winter, with an associated lower risk of hypoxia. However, it is still to determine whether hypoxia is indeed less common during winter, and whether a potentially more stable environment in terms of DO modifies mangrove fish assemblages, either by allowing identified species here to use habitats more extensively, or by allowing new non-identified species here to use mangrove habitats.

This study is the first to link species-specific acute hypoxia tolerance thresholds with patterns of mangrove utilisation. While this information is valuable for management purposes, determining species-specific sublethal hypoxia thresholds would benefit decision-makers as

fish most likely start to respond behaviourally at this threshold. It will provide invaluable information to determine species-specific mangrove value. This study showed that fish commonly using mangrove habitats were very tolerant to hypoxia, and therefore suggests that being hypoxia tolerant is a required adaptation. Testing whether hypoxia tolerance of species known to use adjacent habitats not commonly experiencing diel hypoxia (for instance coral reefs) and not venturing in mangrove habitats, are different than species known to extensively use mangrove habitats, would provide support to this hypothesis. To enhance the ecological relevance of future experimental studies on hypoxia tolerance of estuarine fish, additional stressors should be integrated. Indeed, hypoxia rarely occurs independently in mangroves, but often is coupled with low pH, high temperature, and potential high concentration of toxins such as sulphates, ammonia and methane. It would be very informative to study their combined effects on fish as it is expected that they will lower hypoxia tolerance.

References

Alongi, D.M.: Present state and future of the world's mangrove forests, Environ. Conserv., 29, 2002.

Alongi, D.M., Sasekumar, A., Chong, V.C., Pfitzner, J., Trott, L.A., Tirendi, F., Dixon, P., Brunskill, G.J.: Sediment accumulation and organic material flux in a managed mangrove ecosystem: estimates of land–ocean–atmosphere exchange in peninsular Malaysia, Mar. Geol., 208, 383-402, 2004a.

Alongi, D.M., Wattayakorn, G., Tirendi, F., Dixon, P.: Nutrient capital in different aged forests of the mangrove Rhizophora apiculata, Bot. Mar., 47, 116-124, 2004b.

Alsemgeest, G.P., Dale, P.E.R., Alsemgeest, D.H.: Evaluating the risk of potential acid sulfate soils and habitat modification for mosquito control (runneling) in coastal salt marshes: comparing methods and managing the risk, Environ Manage, 36, 152-161, 2005.

ANZECC/ARMCANZ: National Water Quality Guidelines, Australia New Zealand Environment Conservation Council, 2000.

Argent, D.G., Carline, R.F.: Fish assemblage changes in relation to watershed landuse disturbance, Aquat. Ecosyst. Health Manage., 7, 101-114, 2004.

Augustinus, P.G.E.F.: Chapter 12 Geomorphology and Sedimentology of Mangroves, in: Developments in Sedimentology, edited by: Perillo, G.M.E., Elsevier, 333-357, 1995.

Baker, R., Sheaves, M., Johnston, R.: Geographic variation in mangrove flooding and accessibility for fishes and nektonic crustaceans, Hydrobiologia, 762, 1-14, 2015.

Barletta, M., Saint-Paul, U., Barletta-Bergan, A., Ekau, W., Schories, D.: Spatial and temporal distribution of Myrophis punctatus (Ophichthidae) and associated fish fauna in a northern Brazilian intertidal mangrove forest, Hydrobiologia, 426, 65-74, 2000.

Barnes, L., Bellwood, D.R., Sheaves, M., Tanner, J.K.: The use of clear-water non-estuarine mangroves by reef fishes on the Great Barrier Reef, Mar. Biol., 159, 211-220, 2012.

Baumann, H., Wallace, R.B., Tagliaferri, T., Gobler, C.J.: Large natural pH, CO_2 and O_2 fluctuations in a temperate tidal salt marsh on diel, seasonal, and interannual time scales, Estuar. Coasts, 38, 220-231, 2015.

Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F., Weinstein, M.R.: The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates, Bioscience, 51, 633-641, 2001.

Becker, A., Coppinger, C., Whitfield, A.K.: Influence of tides on assemblages and behaviour of fishes associated with shallow seagrass edges and bare sand, Mar. Ecol. Prog. Ser., 456, 187-199, 2012.

Bell, G.W., Eggleston, D.B.: Species-specific avoidance responses by blue crabs and fish to chronic and episodic hypoxia, Mar. Biol., 146, 761-770, 2005.

Bell, J.D., Pollard, D.A., Burchmore, J.J., Pease, B.C., Middleton, M.J.: Structure of a fish community in a temperate tidal mangrove creek in Botany Bay, New South Wales, Mar. Freshw. Res., 35, 33-46, 1984.

Blaber, S.J.M., Brewer, D.T., Salini, J.P.: Species composition and biomasses of fishes in different habitats of a tropical Northern Australian estuary: Their occurrence in the adjoining sea and estuarine dependence, Estuar. Coast. Shelf Sci., 29, 509-531, 1989.

Borowiec, B.G., Darcy, K.L., Gillette, D.M., Scott, G.R.: Distinct physiological strategies are used to cope with constant hypoxia and intermittent hypoxia in killifish (Fundulus heteroclitus), J. Exp. Biol., 218, 1198-1211, 2015.

Bosire, J.O., Dahdouh-Guebas, F., Walton, M., Crona, B.I., Lewis, R.R., Field, C., Kairo, J.G., Koedam, N.: Functionality of restored mangroves: A review, Aquat. Bot., 89, 251-259, 2008.

Bouillon, S., Borges, A.V., Castañeda-Moya, E., Diele, K., Dittmar, T., Duke, N.C., Kristensen, E., Lee, S.Y., Marchand, C., Middelburg, J.J., Rivera-Monroy, V.H., Smith, T.J., Twilley, R.R.: Mangrove production and carbon sinks: A revision of global budget estimates, Global Biogeochem. Cycles, 22, GB2013, 2008.

Bouillon, S., Middelburg, J.J., Dehairs, F., Borges, A.V., Abril, G., Flindt, M.R., Ulomi, S., Kristensen, E.: Importance of intertidal sediment processes and porewater exchange on the water column biogeochemistry in a pristine mangrove creek (Ras Dege, Tanzania), Biogeosciences, 4, 311-322, 2007.

Bradley, M., Baker, R., Nagelkerken, I., Sheaves, M.: Context is more important than habitat type in determining use by juvenile fish, Landsc. Ecol., 2019.

Brady, D.C., Targett, T.E.: Characterizing the escape response of juvenile summer flounder *Paralichthys dentatus* to diel-cycling hypoxia, J. Fish Biol., 77, 137-152, 2010.

Brady, D.C., Targett, T.E.: Movement of juvenile weakfish *Cynoscion regalis* and spot *Leiostomus xanthurus* in relation to diel-cycling hypoxia in an estuarine tidal tributary, Mar. Ecol. Prog. Ser., 491, 199-219, 2013.

Bray, J.R., Curtis, J.T.: An Ordination of the Upland Forest Communities of Southern Wisconsin, Ecol. Monogr., 27, 325-349, 1957.

Breiman, L.: Random Forests, in: Machine Learning, edited by: Schapire, R.E., Kluwer Academic Publishers, The Netherlands, 5-32, 2001.

Breitburg, D.: Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries, Estuaries, 25, 767-781, 2002.

Breitburg, D., Levin, L.A., Oschlies, A., Grégoire, M., Chavez, F.P., Conley, D.J., Garçon, V., Gilbert, D., Gutiérrez, D., Isensee, K., Jacinto, G.S., Limburg, K.E., Montes, I., Naqvi, S.W.A., Pitcher, G.C., Rabalais, N.N., Roman, M.R., Rose, K.A., Seibel, B.A., Telszewski, M., Yasuhara, M., Zhang, J.: Declining oxygen in the global ocean and coastal waters, Science, 359, eaam7240, 2018.

Breitburg, D.L.: Episodic hypoxia in Chesapeake Bay - Interacting effects of recruitment, behavior, and physical disturbance, Ecol. Monogr., 62, 525-546, 1992.

Breitburg, D.L.: Behavioral response of fish larvae to low dissolved-oxygen concentrations in a stratified water column, Mar. Biol., 120, 615-625, 1994.

Breitburg, D.L., Loher, T., Pacey, C.A., Gerstein, A.: Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web, Ecol. Monogr., 67, 489-507, 1997.

Breitburg, D.L., Steinberg, N., Dubeau, S., Cooksey, C., Houde, E.D.: Effects of low dissolved-oxygen on predation on estuarine fish larvae, Mar. Ecol. Prog. Ser., 104, 235-246, 1994.

Bretsch, K., Allen, D.M.: Tidal migrations of nekton in salt marsh intertidal creeks, Estuar. Coasts, 29, 474-486, 2006.

Buffoni, G., Cappelletti, A.: Oxygen dynamics in a highly trophic aquatic environment. The case of Orbetello coastal lagoon, Estuar. Coast. Shelf Sci., 49, 763-774, 1999.

Burggren, W.W.: "Air Gulping" Improves Blood Oxygen Transport during Aquatic Hypoxia in the Goldfish Carassius auratus, Physiol. Zool., 55, 327-334, 1982.

Burrows, M.T.: Depth selection behaviour during activity cycles of juvenile plaice on a simulated beach slope, J. Fish Biol., 59, 116-125, 2001.

Bush, R.T., Fyfe, D., Sullivan, L.A.: Occurrence and abundance of monosulfidic black ooze in coastal acid sulfate soil landscapes, Soil Res, 42, 609-616, 2004.

Butler, B., Burrows, D.W.: Dissolved oxygen guidelines for freshwater habitats of northern Australia, ACTFR report No. 07/32, Australian Centre for Tropical Freshwater Research, Townsville, 2007.

Butler, B., Burrows, D.W., Pearson, R.: Testing the hypoxia tolerance of tropical freshwater fishes, ACTFR report No. 07/31, Australian Centre for Tropical Freshwater Research, Townsville, 2007.

Call, M., Maher, D.T., Santos, I.R., Ruiz-Halpern, S., Mangion, P., Sanders, C.J., Erler, D.V., Oakes, J.M., Rosentreter, J., Murray, R., Eyre, B.D.: Spatial and temporal variability of carbon dioxide and methane fluxes over semi-diurnal and spring–neap–spring timescales in a mangrove creek, Geochim. Cosmochim. Acta, 150, 211-225, 2015.

Camp, E.F., Nitschke, M.R., Rodolfo-Metalpa, R., Houlbreque, F., Gardner, S.G., Smith, D.J., Zampighi, M., Suggett, D.J.: Reef-building corals thrive within hot-acidified and deoxygenated waters, Sci Rep, 7, 2434, 2017.

Castellanos-Galindo, G.A., Krumme, U., Rubio, E.A., Saint-Paul, U.: Spatial variability of mangrove fish assemblage composition in the tropical eastern Pacific Ocean, Rev. Fish Biol. Fish., 23, 69-86, 2012.

Castellanos-Galindo, G.A., Krumme, U., Willis, T.J.: Tidal influences on fish distributions on tropical eastern Pacific rocky shores (Colombia), Mar. Ecol. Prog. Ser., 416, 241-254, 2010.

Chabot, D., Claireaux, G.: Environmental hypoxia as a metabolic constraint on fish: The case of Atlantic cod, *Gadus morhua*, Mar. Pollut. Bull., 57, 287-294, 2008.

Chabot, D., McKenzie, D.J., Craig, J.F.: Metabolic rate in fishes: definitions, methods and significance for conservation physiology, J. Fish Biol., 88, 1-9, 2016a.

Chabot, D., Steffensen, J.F., Farrell, A.P.: The determination of standard metabolic rate in fishes, J. Fish Biol., 88, 81-121, 2016b.

Chapman, L.J.: Low-Oxygen Lifestyles, in: Extremophile Fishes: Ecology, Evolution, and Physiology of Teleosts in Extreme Environments, edited by: Riesch, R., Tobler, M., Plath, M., Springer International Publishing, Cham, 9-33, 2015.

Chapman, L.J., McKenzie, D.J.: Chapter 2 Behavioral Responses and Ecological Consequences, in: Fish Physiology: Hypoxia, edited by: Jeffrey G. Richards, Farrell, A.P., Colin, J.B., Academic Press, 25-77, 2009.

Claireaux, G., Chabot, D.: Responses by fishes to environmental hypoxia: integration through Fry's concept of aerobic metabolic scope, J. Fish Biol., 88, 232-251, 2016.

Claireaux, G., Webber, D., Kerr, S., Boutilier, R.: Physiology and behaviour of free-swimming Atlantic cod (Gadus morhua) facing fluctuating salinity and oxygenation conditions, J. Exp. Biol., 198, 61, 1995.

Clarke, K., Gorley, R.N. (Eds.): Primer v6: User Manual/Tutorial, Plymouth Marine Laboratory: Plymouth, UK, ; 2006.

Collins, G.M., Clark, T.D., Rummer, J.L., Carton, A.G.: Hypoxia tolerance is conserved across genetically distinct sub-populations of an iconic, tropical Australian teleost (Lates calcarifer), Conserv. Physiol., 1, cot029-cot029, 2013.

Conley, D.J., Carstensen, J., Vaquer-Sunyer, R., Duarte, C.M.: Ecosystem thresholds with hypoxia, Hydrobiologia, 629, 21-29, 2009.

Craig, J.K.: Aggregation on the edge: effects of hypoxia avoidance on the spatial distribution of brown shrimp and demersal fishes in the Northern Gulf of Mexico, Mar. Ecol. Prog. Ser., 445, 75-95, 2012.

Craig, P.M., Fitzpatrick, J.L., Walsh, P.J., Wood, C.M., McClelland, G.B.: Coping with aquatic hypoxia: how the plainfin midshipman (Porichthys notatus) tolerates the intertidal zone, Environ. Biol. Fishes, 97, 163-172, 2014.

Cui, W., Chui, T.F.M.: Temporal variations in water quality in a brackish tidal pond: Implications for governing processes and management strategies, J. Environ. Manage., 193, 108-117, 2017.

D'Avanzo, C., Kremer, J.N.: Diel oxygen dynamics and anoxic events in an eutrophic estuary of Waquoit Bay, Massachusetts, Estuaries, 17, 131-139, 1994.

D'Autilia, R., Falcucci, M., Hull, V., Parrella, L.: Short time dissolved oxygen dynamics in shallow water ecosystems, Ecol. Model., 179, 297-306, 2004.

Dale, P.E., Knight, J.M., Dwyer, P.G.: Mangrove rehabilitation: a review focusing on ecological and institutional issues, Wetlands Ecol. Manage., 22, 587-604, 2014.

Dantas, D.V., Barletta, M., Araújo Lima, A.R., De Assis Almeida Ramos, J., Da Costa, M.F., Saint-Paul, U.: Nursery habitat shifts in an estuarine ecosystem: patterns of use by sympatric catfish species, Estuar. Coasts, 35, 587-602, 2012.

Das, S.: Ecological Restoration and Livelihood: Contribution of Planted Mangroves as Nursery and Habitat for Artisanal and Commercial Fishery, World Development, 94, 492-502, 2017.

Das, T., Stickle, W.B.: Detection and avoidance of hypoxic water by juvenile Callinectes sapidus and C. similis, Mar. Biol., 120, 593-600, 1994.

Dauer, D.M.: Biological criteria, environmental health and estuarine macrobenthic community structure, Mar. Pollut. Bull., 26, 249-257, 1993.

David, F., Marchand, C., Taillardat, P., Thành-Nho, N., Meziane, T.: Nutritional composition of suspended particulate matter in a tropical mangrove creek during a tidal cycle (Can Gio, Vietnam), Estuar. Coast. Shelf Sci., 200, 126-130, 2018.

Davis, B., Baker, R., Sheaves, M.: Seascape and metacommunity processes regulate fish assemblage structure in coastal wetlands, Mar. Ecol. Prog. Ser., 500, 187-202, 2014a.

Davis, B., Johnston, R., Baker, R., Sheaves, M.: Fish utilisation of wetland nurseries with complex hydrological connectivity, PLoS ONE, 7, e49107, 2012.

Davis, B., Mattone, C., Sheaves, M.: Bottom-up control regulates patterns of fish connectivity and assemblage structure in coastal wetlands, Mar. Ecol. Prog. Ser., 500, 175-186, 2014b.

Davis, T.L.O.: Temporal changes in the fish fauna entering a tidal swamp system in tropical Australia, Environ. Biol. Fishes, 21, 161-172, 1988.

Del Toro-Silva, F.M., Miller, J.M., Taylor, J.C., Ellis, T.A.: Influence of oxygen and temperature on growth and metabolic performance of *Paralichthys lethostigma* (Pleuronectiformes: Paralichthyidae), J. Exp. Mar. Biol. Ecol., 358, 113-123, 2008.

Diaz, R.J.: Overview of hypoxia around the world, J. Environ. Qual., 30, 275-281, 2001.

Diaz, R.J., Breitburg, D.L.: Chapter 1 The Hypoxic Environment, in: Fish Physiology: Hypoxia, edited by: Jeffrey G. Richards, Farrell, A.P., Colin, J.B., Academic Press, 1-23, 2009.

Diaz, R.J., Neubauer, R.J., Schaffner, L.C., Pihl, L., Baden, S.P.: Continuous monitoring of dissolved oxygen in an estuary experiencing periodic hypoxia and the effect of hypoxia on macrobenthos and fish, in: Marine Coastal Eutrophication, edited by: Vollenweider, R.A., Marchetti, R., Viviani, R., Elsevier, Amsterdam, 1055-1068, 1992.

Diaz, R.J., Rosenberg, R.: Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna, in: Oceanography and Marine Biology - An Annual Review, edited by: Ansell, A.D., Gibson, R.N., Barnes, M., UCL Press, London, 245-303, 1995.

Diaz, R.J., Rosenberg, R.: Spreading dead zones and consequences for marine ecosystems, Science, 321, 926-929, 2008.

Dittmar, T., Hertkorn, N., Kattner, G., Lara, R.J.: Mangroves, a major source of dissolved organic carbon to the oceans, Global Biogeochem. Cycles, 20, GB1012, 2006.

Dorenbosch, M., Grol, M.G.G., Christianen, M.J.A., Nagelkerken, I., van der Velde, G.: Indo-Pacific seagrass beds and mangroves contribute to fish density coral and diversity on adjacent reefs, Mar. Ecol. Prog. Ser., 302, 63-76, 2005.

Dorenbosch, M., Verberk, W., Nagelkerken, I., van der Velde, G.: Influence of habitat configuration on connectivity between fish assemblages of Caribbean seagrass beds, mangroves and coral reefs, Mar. Ecol. Prog. Ser., 334, 103-116, 2007.

Driedzic, W.R., Hochachka, P.W.: Metabolism in Fish During Exercise, in: Fish Physiology, edited by: Hoar, W.S., Randall, D.J., Academic Press, Inc., New York, 503-543, 1978.

Duke, N.C., Ball, M.C., Ellison, J.C.: Factors Influencing Biodiversity and Distributional Gradients in Mangroves, Global Ecol. Biogeogr. Lett., 7, 27-47, 1998.

Dunbar, K., Baker, R., Sheaves, M.: Effects of forest width on fish use of fringing mangroves in a highly urbanised tropical estuary, Mar. Freshw. Res., 68, 1764-1770, 2017.

Eby, L.A., Crowder, L.B.: Hypoxia-based habitat compression in the Neuse River Estuary: context-dependent shifts in behavioral avoidance thresholds, Can. J. Fish. Aquat. Sci., 59, 952-965, 2002.

Eby, L.A., Crowder, L.B., McClellan, C.M., Peterson, C.H., Powers, M.J.: Habitat degradation from intermittent hypoxia: impacts on demersal fishes, Mar. Ecol. Prog. Ser., 291, 249-262, 2005a.

Eby, L.A., Crowder, L.B., McClellan, C.M., Peterson, C.H., Powers, M.J.: Habitat degradation from intermittent hypoxia: impacts on demersal fishes, Mar. Ecol. Prog. Ser., 291, 249-261, 2005b.

Ehrenfeld, J.G.: Evaluating wetlands within an urban context, Ecol Eng, 15, 253-265, 2000.

Elliott, M., Quintino, V.: The Estuarine Quality Paradox, Environmental Homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas, Mar. Pollut. Bull., 54, 640-645, 2007.

Ellis, W.L., Bell, S.S.: Tidal influence on a fringing mangrove intertidal fish community as observed by in situ video recording: implications for studies of tidally migrating nekton, Mar. Ecol. Prog. Ser., 370, 207-219, 2008.

Fagernes, C.E., Stensløkken, K.-O., Røhr, Å.K., Berenbrink, M., Ellefsen, S., Nilsson, G.E.: Extreme anoxia tolerance in crucian carp and goldfish through neofunctionalization of duplicated genes creating a new ethanol-producing pyruvate decarboxylase pathway, Scientific Reports, 7, 7884, 2017.

Falkowski, P.G., Raven, J.A. (Eds.): Aquatic photosynthesis, Malden Mass., Blackwell Science, Oxford, 1997.

Faunce, C.H., Serafy, J.E.: Mangroves as fish habitat: 50 years of field studies, Mar. Ecol. Prog. Ser., 318, 1-18, 2006.

Flint, N., Crossland, M.R., Pearson, R.G.: Sublethal effects of fluctuating hypoxia on juvenile tropical Australian freshwater fish, Mar. Freshw. Res., 66, 293-304, 2015.

Francis, F.T., Côté, I.M.: Fish movement drives spatial and temporal patterns of nutrient provisioning on coral reef patches, Ecosphere, 9, e02225, 2018.

Froelich, P.N., Klinkhammer, G.P., Bender, M.L., Luedtke, N.A., Heath, G.R., Cullen, D., Dauphin, P., Hammond, D., Hartman, B., Maynard, V.: Early oxidation of organic matter in pelagic sediments of the eastern equatorial Atlantic: suboxic diagenesis, Geochim. Cosmochim. Acta, 43, 1075-1090, 1979.

Froese, R., Pauly, D. Fishbase: http://www.fishbase.org, last access: 4 December 2017.

Fry, F.E.J. (Eds.): Effects of the environment on animal activity., University of Toronto Press, Toronto, 1947.

Fry, F.E.J. (Eds.): The Effect of Environmental Factors on the Physiology of Fish, University of Toronto Press, Toronto, 1971.

Furukawa, K., Wolanski, E., Mueller, H.: Currents and Sediment Transport in Mangrove Forests, Estuar. Coast. Shelf Sci., 44, 301-310, 1997.

Gaesser, G.A., Brooks, G.A.: Metabolic bases of excess post-exercise oxygen consumption: a review, Med. Sci. Sports Exerc., 16, 1984.

Gallo, N.D., Levin, L.A., Beckwith, M., Barry, J.P.: Home sweet suboxic home: remarkable hypoxia tolerance in two demersal fish species in the Gulf of California, Ecology, 100, 5, 2019.

Garcia, H.E., Gordon, L.I.: Oxygen solubility in seawater: Better fitting equations, Limnol. Oceanogr., 37, 1307-1312, 1992.

Gedan, K.B., Altieri, A.H., Feller, I., Burrell, R., Breitburg, D.: Community composition in mangrove ponds with pulsed hypoxic and acidified conditions, Ecosphere, 8, e02053, 2017.

Gibson, R.N.: Go with the flow: tidal migration in marine animals, Hydrobiologia, 503, 153-161, 2003.

Gleeson, J., Santos, I.R., Maher, D.T., Golsby-Smith, L.: Groundwater-surface water exchange in a mangrove tidal creek: Evidence from natural geochemical tracers and implications for nutrient budgets, Mar. Chem., 156, 27-37, 2013.

Greaney, G.S., Place, A.R., Cashon, R.E., Smith, G., Powers, D.A.: Time course of changes in enzyme-activities and blood respiratory properties of killifish during long-term acclimation to hypoxia, Physiol. Zool., 53, 136-144, 1980.

Guppy, M., Withers, P.: Metabolic depression in animals: physiological perspectives and biochemical generalizations, Biol. Rev., 74, 1-40, 1999.

Hampel, H., Cattrijsse, A., Vincx, M.: Tidal, diel and semi-lunar changes in the faunal assemblage of an intertidal salt marsh creek, Estuar Coast Shelf Sci, 56, 795-805, 2003.

Harborne, A.R., Mumby, P.J., Micheli, F., Perry, C.T., Dahlgren, C.P., Holmes, K.E., Brumbaugh, D.R.: The Functional Value of Caribbean Coral Reef, Seagrass and Mangrove Habitats to Ecosystem Processes, Adv. Mar. Biol., 50, 57-189, 2006.

Harborne, A.R., Talwar, B., Brooks, E.J.: The conservation implications of spatial and temporal variability in the diurnal use of Bahamian tidal mangrove creeks by transient predatory fishes, Aquat. Conserv.: Mar. Freshwat. Ecosyst., 26, 202-211, 2016.

Helmuth, B.: From cells to coastlines: how can we use physiology to forecast the impacts of climate change?, J. Exp. Biol., 212, 753, 2009.

Hilton, Z., Wellenreuther, M., Clements, K.D.: Physiology underpins habitat partitioning in a sympatric sister-species pair of intertidal fishes, Funct. Ecol., 22, 1108-1117, 2008.

Hogarth, P.J. (Eds.): The Biology of Mangroves, Oxford University Press, 1999.

Hothorn, T., Hornik, K., Zeileis, A.: Party: A Laboratory for Recursive Part(y)itioning, R package version 0.9–9999, http://cran.r-project.org/package=party, 2010

Hull, V., Mocenni, C., Falcucci, M., Marchettini, N.: A trophodynamic model for the lagoon of Fogliano (Italy) with ecological dependent modifying parameters, Ecol. Model., 134, 153-167, 2000.

Hunt, R.J., Christiansen, I.H.: Understanding dissolved oxygen in streams, CRC Sugar Technical Publication, , Townsville, 2000.

Igulu, M.M., Nagelkerken, I., Dorenbosch, M., Grol, M.G.G., Harborne, A.R.: Mangrove habitat use by juvenile reef fish: meta-analysis reveals that tidal regime matters more than biogeographic region, PLoS ONE, 9, e114715, 2014.

Illing, B., Rummer, J.L.: Physiology can contribute to better understanding, management, and conservation of coral reef fishes, Conserv. Physiol., 5, 2017.

Iwatsuki, Y., Kimura, S., Yoshino, T.: A new sparid, *Acanthopagrus akazakii*, from New Caledonia with notes on nominal species of *Acanthopagrus*, Ichthyol. Res., 53, 406-414, 2006.

Iwatsuki, Y., Kume, M., Yoshino, T.: A new species, *Acanthopagrus pacificus* from the Western Pacific (Pisces, Sparidae), Bull. Natl. Mus. Nat. Sci., 36, 115-130, 2010.

James, C.S., Reside, A.E., VanDerWal, J., Pearson, R.G., Burrows, D., Capon, S.J., Harwood, T.D., Hodgson, L., Waltham, N.J.: Sink or swim? Potential for high faunal turnover in Australian rivers under climate change, J. Biogeogr., 44, 489-501, 2017.

Johnston, R., Sheaves, M.: Small fish and crustaceans demonstrate a preference for particular small-scale habitats when mangrove forests are not accessible, J. Exp. Mar. Biol. Ecol., 353, 164-179, 2007.

Jourdan-Pineau, H., Dupont-Prinet, A., Claireaux, G., McKenzie, David J.: An Investigation of Metabolic Prioritization in the European Sea Bass, *Dicentrarchus labrax*, Physiol. Biochem. Zool., 83, 68-77, 2010.

Kathiresan, K., Bingham, B.L.: Biology of mangroves and mangrove ecosystems, in: Advances in Marine Biology, Vol 40, edited by: Southward, A.J., Tyler, P.A., Young, C.M., Fuiman, L.A., Academic Press Ltd-Elsevier Science Ltd, London, 81-251, 2001.

Keeling, R.F., Körtzinger, A., Gruber, N.: Ocean Deoxygenation in a Warming World, Ann. Rev. Mar. Sci., 2, 199-229, 2009.

Kenney, B.E., Litaker, W., Duke, C.S., Ramus, J.: Community oxygen metabolism in a shallow tidal estuary, Estuar. Coast. Shelf Sci., 27, 33-43, 1988.

Kerr, J.L., Baldwin, D.S., Whitworth, K.L.: Options for managing hypoxic blackwater events in river systems: A review, J. Environ. Manage., 114, 139-147, 2013.

Killen, S.S., Marras, S., Metcalfe, N.B., McKenzie, D.J., Domenici, P.: Environmental stressors alter relationships between physiology and behaviour, Trends Ecol. Evol., 28, 651-658, 2013.

Kimball, M.E., Able, K.W.: Tidal Migrations of Intertidal Salt Marsh Creek Nekton Examined with Underwater Video, Northeast. Nat., 19, 475-486, 2012.

Knight, J.M., Griffin, L., Dale, P.E.R., Sheaves, M.: Short-term dissolved oxygen patterns in sub-tropical mangroves, Estuar. Coast. Shelf Sci., 131, 290-296, 2013.

Knudson, C., Geyer, C.J., Benson, S.: Generalized Linear Mixed Models via Monte Carlo Likelihood Approximation. R Package Version. 1.3.0., 2018.

Kramer, D.L.: Dissolved oxygen and fish behavior, Environ. Biol. Fishes, 18, 81-92, 1987.

Kramer, D.L., McClure, M.: Aquatic surface respiration, a widespread adaptation to hypoxia in tropical freshwater fishes, Environ. Biol. Fishes, 7, 47-55, 1982.

Krumme, U.: Patterns in tidal migration of fish in a Brazilian mangrove channel as revealed by a split-beam echosounder, Fish. Res., 70, 1-15, 2004.

Krumme, U.: Diel and Tidal Movements by Fish and Decapods Linking Tropical Coastal Ecosystems, in: Ecological Connectivity among Tropical Coastal Ecosystems, edited by: Nagelkerken, I., Dordrecht; , 271-324, 2009.

Krumme, U., Herbeck, L.S., Wang, T.: Tide- and rainfall-induced variations of physical and chemical parameters in a mangrove-depleted estuary of East Hainan (South China Sea), Mar. Environ. Res., 82, 28-39, 2012.

Krumme, U., Saint-Paul, U., Rosenthal, H.: Tidal and diel changes in the structure of a nekton assemblage in small intertidal creeks in northern Brazil, Aquat. Living Resour., 17, 215-229, 2004.

Laegdsgaard, P., Johnson, C.: Why do juvenile fish utilise mangrove habitats?, J. Exp. Mar. Biol. Ecol., 257, 229-253, 2001.

Lal, P.N.: Coastal fisheries and the management of mangrove resources in Fiji, SPC Fisheries Newsletter, 31, 15-23, 1984.

Laroche, J., Baran, E., Rasoanandrasana, N.B.: Temporal patterns in a fish assemblage of a semiarid mangrove zone in Madagascar, J. Fish Biol., 51, 3-20, 1997.

Lawton, J.H.: From Physiology to Population Dynamics and Communities, Funct. Ecol., 5, 155-161, 1991.

Lee, S.Y., Dunn, R.J.K., Young, R.A., Connolly, R.M., Dale, P.E.R., Dehayr, R., Lemckert, C.J., McKinnon, S., Powell, B., Teasdale, P.R., Welsh, D.T.: Impact of urbanization on coastal wetland structure and function, Austral Ecol., 31, 149-163, 2006.

Lee, S.Y., Primavera, J.H., Dahdouh-Guebas, F., McKee, K., Bosire, J.O., Cannicci, S., Diele, K., Fromard, F., Koedam, N., Marchand, C., Mendelssohn, I., Mukherjee, N., Record, S.: Ecological role and services of tropical mangrove ecosystems: a reassessment, Global Ecol. Biogeogr., 23, 726-743, 2014.

Lefcheck, J.S., Hughes, B.B., Johnson, A.J., Pfirrmann, B.W., Rasher, D.B., Smyth, A.R., Williams, B.L., Beck, M.W., Orth, R.J.: Are coastal habitats important nurseries? A meta-analysis, Conserv. Lett., e12645, 2019.

Leopold, A., Marchand, C., Deborde, J., Allenbach, M.: Water Biogeochemistry of a Mangrove-Dominated Estuary Under a Semi-Arid Climate (New Caledonia), Estuar. Coasts, 40, 773-791, 2017.

Levin, L.A., Ekau, W., Gooday, A.J., Jorissen, F., Middelburg, J.J., Naqvi, S.W.A., Neira, C., Rabalais, N.N., Zhang, J.: Effects of natural and human-induced hypoxia on coastal benthos, Biogeosciences, 6, 2063-2098, 2009.

Lewis, R.R., Gilmore, R.G.: Important considerations to achieve successful mangrove forest restoration with optimum fish habitat, Bull. Mar. Sci., 80, 823-837, 2007.

Li, X.Y., Hu, B.X., Burnett, W.C., Santos, I.R., Chanton, J.P.: Submarine Ground Water Discharge Driven by Tidal Pumping in a Heterogeneous Aquifer, Ground Water, 47, 558-568, 2009.

Lin, C., Wood, M., Haskins, P., Ryffel, T., Lin, J.: Controls on water acidification and de-oxygenation in an estuarine waterway, eastern Australia, Estuar. Coast. Shelf Sci., 61, 55-63, 2004.

Liu, G., Wang, A., Wang, X., Liu, P.: A Review of Artificial Lateral Line in Sensor Fabrication and Bionic Applications for Robot Fish, Applied bionics and biomechanics, 2016, 4732703-4732703, 2016.

Lukacs, G.: Wetlands of the Townsville area, ACTFR report No. 96/28, Australian Centre for Tropical Freshwater Research, Townsville, 1996.

Maher, D.T., Santos, I.R., Golsby-Smith, L., Gleeson, J., Eyre, B.D.: Groundwater-derived dissolved inorganic and organic carbon exports from a mangrove tidal creek: The missing mangrove carbon sink?, Limnol. Oceanogr., 58, 475-488, 2013.

Mandal, S., Debnath, M., Ray, S., Ghosh, P.B., Roy, M., Ray, S.: Dynamic modelling of dissolved oxygen in the creeks of Sagar island, Hooghly–Matla estuarine system, West Bengal, India, Appl. Math. Model., 36, 5952-5963, 2012.

Mandic, M., Regan, M.D.: Can variation among hypoxic environments explain why different fish species use different hypoxic survival strategies?, J. Exp. Biol., 221, jeb161349, 2018.

Mandic, M., Todgham, A.E., Richards, J.G.: Mechanisms and evolution of hypoxia tolerance in fish, Proc. R. Soc. B, 276, 735-744, 2009.

Mangora, M.M.: Poverty and institutional management stand-off: a restoration and conservation dilemma for mangrove forests of Tanzania, Wetlands Ecol. Manage., 19, 533-543, 2011.

Marchand, C., Baltzer, F., Lallier-Vergès, E., Albéric, P.: Pore-water chemistry in mangrove sediments: relationship with species composition and developmental stages (French Guiana), Mar. Geol., 208, 361-381, 2004.

Marchand, C., Lallier-Vergès, E., Allenbach, M.: Redox conditions and heavy metals distribution in mangrove forests receiving effluents from shrimp farms (Teremba Bay, New Caledonia), J. Soils Sed., 11, 529-541, 2011.

Mattone, C.: Benthic infauna of mangrove forests: dissolved oxygen and environmental settings determine their community composition and function, PhD, James Cook University, Townsville, 2016.

Mattone, C., Sheaves, M.: Patterns, drivers and implications of dissolved oxygen dynamics in tropical mangrove forests, Estuar. Coast. Shelf Sci., 197, 205-213, 2017.

Mazda, Y., Sato, Y., Sawamoto, S., Yokochi, H., Wolanski, E.: Links between physical, chemical and biological processes in Bashita-minato, a mangrove swamp in Japan, Estuar. Coast. Shelf Sci., 31, 817-833, 1990.

McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M.: Rebuilding community ecology from functional traits, Trends Ecol. Evol., 21, 178-185, 2006.

McNeil, D.G., Closs, G.P.: Behavioural responses of a south-east Australian floodplain fish community to gradual hypoxia, Freshw Biol, 52, 412-420, 2007.

Mercier, L., Darnaude, A.M., Bruguier, O., Vasconcelos, R.P., Cabral, H.N., Costa, M.J., Lara, M., Jones, D.L., Mouillot, D.: Selecting statistical models and variable combinations for optimal classification using otolith microchemistry, Ecol. Appl., 21, 1352-1364, 2011.

Meynecke, J.-O., Poole, G.C., Werry, J., Lee, S.Y.: Use of PIT tag and underwater video recording in assessing estuarine fish movement in a high intertidal mangrove and salt marsh creek, Estuar. Coast. Shelf Sci., 79, 168-178, 2008.

Mogdans, J., Bleckmann, H.: Coping with flow: behavior, neurophysiology and modeling of the fish lateral line system, Biol. Cybern., 106, 627-642, 2012.

Mumby, P.J., Edwards, A.J., Arias-Gonzalez, J.E., Lindeman, K.C., Blackwell, P.G., Gall, A., Gorczynska, M.I., Harborne, A.R., Pescod, C.L., Renken, H., Wabnitz, C.C.C., Llewellyn, G.: Mangroves enhance the biomass of coral reef fish communities in the Caribbean, Nature, 427, 533-536, 2004.

Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.O., Pawlik, J., Penrose, H.M., Sasekumar, A., Somerfield, P.J.: The habitat function of mangroves for terrestrial and marine fauna: A review, Aquat. Bot., 89, 155-185, 2008.

Nagelkerken, I., Dorenbosch, M., Verberk, W.C.E.P., Morinière, E.C.d.l., Velde, G.v.d.: Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution, Mar. Ecol. Prog. Ser., 202, 175-192, 2000a.

Nagelkerken, I., Faunce, C.H.: Colonisation of artificial mangroves by reef fishes in a marine seascape, Estuar. Coast. Shelf Sci., 75, 417-422, 2007.

Nagelkerken, I., Faunce, C.H.: What makes mangroves attractive to fish? Use of artificial units to test the influence of water depth, cross-shelf location, and presence of root structure, Estuar. Coast. Shelf Sci., 79, 559-565, 2008.

Nagelkerken, I., Kleijnen, S., Klop, T., Brand, R.A.C.J.v.d., MoriniÃƒÂ¨re, E.C.d.l., Velde, G.v.d.: Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds, Mar. Ecol. Prog. Ser., 214, 225-235, 2001.

Nagelkerken, I., Roberts, C., van der Velde, G., Dorenbosch, M., van Riel, M.C., Cocheret de la Morinière, E., Nienhuis, P.: How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale, Mar. Ecol. Prog. Ser., 244, 299-305, 2002.

Nagelkerken, I., Sheaves, M., Baker, R., Connolly, R.M.: The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna, Fish Fish. Res. (Resour. Fish. Manage. Syst.: Rep. Sci. News), 2013.

Nagelkerken, I., van der Velde, G., Gorissen, M.W., Meijer, G.J., van't Hof, T., den Hartog, C.: Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique, Estuar Coast Shelf Sci, 51, 31-44, 2000b.

Nelson, B.W., Sasekumar, A., Ibrahim, Z.Z.: Neap-spring tidal effects on dissolved oxygen in two Malaysian estuaries, Hydrobiologia, 285, 7-17, 1994.

Nelson, J.A.: Oxygen consumption rate v. rate of energy utilization of fishes: a comparison and brief history of the two measurements, J. Fish Biol., 88, 10-25, 2016.

Nezlin, N.P., Kamer, K., Hyde, J., Stein, E.D.: Dissolved oxygen dynamics in a eutrophic estuary, Upper Newport Bay, California, Estuar. Coast. Shelf Sci., 82, 139-151, 2009.

Nilsson, G.E.: Gill remodeling in fish – a new fashion or an ancient secret?, J. Exp. Biol., 210, 2403, 2007.

Nilsson, G.E., Hobbs, J.P., Munday, P.L., Ostlund-Nilsson, S.: Coward or braveheart: extreme habitat fidelity through hypoxia tolerance in a coral-dwelling goby, J. Exp. Biol., 207, 33-39, 2004.

Nilsson, G.E., Ostlund-Nilsson, S.: Hypoxia in paradise: widespread hypoxia tolerance in coral reef fishes, Proc. R. Soc. B, 271, S30-33, 2004.

Nilsson, G.E., Östlund-Nilsson, S.: Does size matter for hypoxia tolerance in fish?, Biol. Rev., 83, 173-189, 2008.

Nixon, S.W.: Coastal marine eutrophication - a definition, social causes, and future concerns, Ophelia, 41, 199-219, 1995.

Norin, T., Malte, H., Clark, T.D.: Differential plasticity of metabolic rate phenotypes in a tropical fish facing environmental change, Funct. Ecol., 30, 369-378, 2016.

Okamura, K., Tanaka, K., Siow, R., Man, A., Kodama, M., Ichikawa, T.: Spring tide hypoxia with relation to chemical properties of the sediments in the Matang mangrove estuary, Malaysia, Jpn Agric Res Q, 44, 325-333, 2010.

Olds, A.D., Albert, S., Maxwell, P.S., Pitt, K.A., Connolly, R.M.: Mangrove-reef connectivity promotes the effectiveness of marine reserves across the western Pacific, Global Ecol. Biogeogr., 22, 1040-1049, 2013.

Olds, A.D., Connolly, R.M., Pitt, K.A., Maxwell, P.S.: Habitat connectivity improves reserve performance, Conserv. Lett., 5, 56-63, 2012.

Paillon, C., Wantiez, L., Kulbicki, M., Labonne, M., Vigliola, L.: Extent of mangrove nursery habitats determines the geographic distribution of a coral reef fish in a South-Pacific archipelago, PLoS ONE, 9, e105158, 2014.

Peña, M.A., Katsev, S., Oguz, T., Gilbert, D.: Modeling dissolved oxygen dynamics and hypoxia, Biogeosciences, 7, 933-957, 2010.

Perna, C., Burrows, D.: Improved dissolved oxygen status following removal of exotic weed mats in important fish habitat lagoons of the tropical Burdekin River floodplain, Australia, Mar. Pollut. Bull., 51, 138-148, 2005.

Petersen, J.K., Pihl, L.: Responses to hypoxia of plaice, Pleuronectes platessa, and dab, Limanda limanda, in the south-east Kattegat: distribution and growth, Environ. Biol. Fishes, 43, 311-321, 1995.

Peterson, M.S.: Hypoxia-induced physiological-changes in two mangrove swamp fishes: sheepshead minnow, *Cyprinodon variegatus* Lacepede and sailfin molly, *Poecilia latipinna* (Lesueur), Comp. Biochem. Physiol. A-Physiol., 97, 17-21, 1990.

Pihl, L.: Changes in the diet of demersal fish due to eutrophication-induced hypoxia in the Kattegat, Sweden, Can. J. Fish. Aquat. Sci., 51, 321-336, 1994.

Pihl, L., Baden, S.P., Diaz, R.J.: Effects of periodic hypoxia on distribution of demersal fish and crustaceans, Mar. Biol., 108, 349-360, 1991.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Team, R.C.: nlme: linear and nonlinear mixed effects models; R package version 3.1-120, 2015.

Pollock, M.S., Clarke, L.M.J., Dubé, M.G.: The effects of hypoxia on fishes: from ecological relevance to physiological effects, Environ. Rev., 15, 1-14, 2007.

Quinn, N.J., Kojis, B.J.: Does the presence of coral reefs in proximity to a tropical estuary affect the estuarine fish assemblage?, Proc. 5th Int. Coral Reef Congr., 5, 445-450, 1985.

R Core Team: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/ (accessed May 2019), 2014.

Rabalais, N.N., Diaz, R.J., Levin, L.A., Turner, R.E., Gilbert, D., Zhang, J.: Dynamics and distribution of natural and human-caused hypoxia, Biogeosciences, 7, 585-619, 2010.

Rabalais, N.N., Turner, R.E., Wiseman, W.J.: Gulf of Mexico Hypoxia, A.K.A. "the Dead Zone", Annu. Rev. Ecol. Syst., 33, 235-263, 2002.

Rahel, F.J., Nutzman, J.W.: Foraging in a Lethal Environment: Fish Predation in Hypoxic Waters of a Stratified Lake, Ecology, 75, 1246-1253, 1994.

Ramos, J.A.A., Barletta, M., Dantas, D.V., Lima, A.R.A., Costa, M.F.: Influence of moon phase on fish assemblages in estuarine mangrove tidal creeks, J. Fish Biol., 78, 344-354, 2011.

Regan, M.D., Mandic, M., Dhillon, R.S., Lau, G.Y., Farrell, A.P., Schulte, P.M., Seibel, B.A., Speers-Roesch, B., Ultsch, G.R., Richards, J.G.: Don't throw the fish out with the respirometry water, J. Exp. Biol., 222, jeb200253, 2019.

Reis-Filho, J.A., Giarrizzo, T., Barros, F.: Tidal migration and cross-habitat movements of fish assemblage within a mangrove ecotone, Mar. Biol., 163, 111, 2016.

Reis, J.A., Giarrizzo, T., Barros, F.: Tidal migration and cross-habitat movements of fish assemblage within a mangrove ecotone, Mar. Biol., 163, 13, 2016.

Richards, J.G.: Chapter 10 Metabolic and Molecular Responses of Fish to Hypoxia, in: Fish Physiology: Hypoxia, edited by: Richards, J.G., Farrell, A.P., Brauner, C.J., Academic Press, 443-485, 2009.

Robertson, A.I., Duke, N.C.: Mangrove fish-communities in tropical Queensland, Australia: Spatial and temporal patterns in densities, biomass and community structure, Mar. Biol., 104, 369-379, 1990.

Rogers, N.J., Urbina, M.A., Reardon, E.E., McKenzie, D.J., Wilsonl, R.W.: A new analysis of hypoxia tolerance in fishes using a database of critical oxygen level (P_{crit}), Conserv. Physiol., 4, cow012, 2016.

Rosenberg, R.: Eutrophication - The future marine coastal nuisance?, Mar. Pollut. Bull., 16, 227-231, 1985.

Rountree, R.A., Able, K.W.: Spatial and temporal habitat use patterns for salt marsh nekton: implications for ecological functions, Aquat. Ecol., 41, 25-45, 2007.

Roy, A.H., Rosemond, A.D., Paul, M.J., Leigh, D.S., Wallace, J.B.: Stream macroinvertebrate response to catchment urbanisation (Georgia, U.S.A.), Freshw Biol, 48, 329-346, 2003.

Rozas, L.P., Minello, T.J.: Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: A review of sampling design with focus on gear selection, Estuaries, 20, 199-213, 1997.

Ruggerone, G.: Differential survival of juvenile sockeye and coho salmon exposed to low dissolved oxygen during winter, J. Fish Biol., 56, 1013-1016, 2000.

Rummer, J.L., Brauner, C.J.: Root Effect Haemoglobins in Fish May Greatly Enhance General Oxygen Delivery Relative to Other Vertebrates, PLoS ONE, 10, e0139477, 2015.

Rummer, J.L., McKenzie, D.J., Innocenti, A., Supuran, C.T., Brauner, C.J.: Root Effect Hemoglobin May Have Evolved to Enhance General Tissue Oxygen Delivery, Science, 340, 1327, 2013.

Sammut, J., White, I., Melville, M.: Acidification of an estuarine tributary in eastern Australia due to drainage of acid sulfate soils, Mar. Freshw. Res., 47, 669-684, 1996.

Schurmann, H., Claireaux, G., Chartois, H.: Changes in vertical distribution of sea bass (Dicentrarchus labrax L.) during a hypoxic episode, Hydrobiologia, 372, 207-213, 1998.

Sedberry, G.R., Carter, J.: The Fish Community of a Shallow Tropical Lagoon in Belize, Central America, Estuaries, 16, 198-215, 1993.

Sheaves, M.: Nature and consequences of biological connectivity in mangrove systems, Mar. Ecol. Prog. Ser., 302, 293-305, 2005.

Sheaves, M.: Ecosystem equivalence and the ability to generalise: insights from global consistencies in mangrove fish assemblages, Mar. Ecol. Prog. Ser., 461, 137-+, 2012.

Sheaves, M.: How many fish use mangroves? The 75% rule an ill-defined and poorly validated concept, Fish Fish., 18, 778-789, 2017.

Sheaves, M., Abrantes, K., Johnston, R.: Nursery ground value of an endangered wetland to juvenile shrimps, Wetlands Ecol. Manage., 15, 311-327, 2007a.

Sheaves, M., Brookes, J., Coles, R., Freckelton, M., Groves, P., Johnston, R., Winberg, P.: Repair and revitalisation of Australia's tropical estuaries and coastal wetlands: Opportunities

and constraints for the reinstatement of lost function and productivity, Mar. Policy, 47, 23-38, 2014.

Sheaves, M., Johnston, R.: Influence of marine and freshwater connectivity on the dynamics of subtropical estuarine wetland fish metapopulations, Mar. Ecol. Prog. Ser., 357, 225-243, 2008.

Sheaves, M., Johnston, R., Abrantes, K.: Fish fauna of dry tropical and subtropical estuarine floodplain wetlands, Mar. Freshw. Res., 58, 931-943, 2007b.

Sheaves, M., Johnston, R., Baker, R.: Use of mangroves by fish: new insights from in-forest videos, Mar. Ecol. Prog. Ser., 549, 167-182, 2016.

Sheaves, M., Molony, B.: Short-circuit in the mangrove food chain, Mar. Ecol. Prog. Ser., 199, 97-109, 2000.

Shoji, J., Masuda, R., Yamashita, Y., Tanaka, M.: Effect of low dissolved oxygen concentrations on behavior and predation rates on red sea bream *Pagrus major* larvae by the jellyfish *Aurelia aurita* and by juvenile Spanish mackerel *Scomberomorus niphonius*, Mar. Biol., 147, 863-868, 2005.

SHOM (Service hydrographique et oceanique de la marine): https://www.shom.fr, last access: 1 March 2017.

Smith, K.J., Able, K.W.: Dissolved oxygen dynamics in salt marsh pools and its potential impacts on fish assemblages, Mar. Ecol. Prog. Ser., 258, 223-232, 2003.

Sokolova, I.M.: Energy-Limited Tolerance to Stress as a Conceptual Framework to Integrate the Effects of Multiple Stressors, Integr. Comp. Biol., 53, 597-608, 2013.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A., Robertson, J.: Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas, Bioscience, 57, 573-583, 2007.

Speers-Roesch, B., Mandic, M., Groom, D.J.E., Richards, J.G.: Critical oxygen tensions as predictors of hypoxia tolerance and tissue metabolic responses during hypoxia exposure in fishes, J. Exp. Mar. Biol. Ecol., 449, 239-249, 2013.

Steckbauer, A., Duarte, C.M., Carstensen, J., Vaquer-Sunyer, R., Conley, D.J.: Ecosystem impacts of hypoxia: thresholds of hypoxia and pathways to recovery, Environmental Research Letters, 6, 025003, 2011.

Steffensen, J.F.: Some errors in respirometry of aquatic breathers: How to avoid and correct for them, Fish Physiol. Biochem., 6, 49-59, 1989.

Stierhoff, K.L., Targett, T.E., Power, J.H.: Hypoxia-induced growth limitation of juvenile fishes in an estuarine nursery: assessment of small-scale temporal dynamics using RNA:DNA, Can. J. Fish. Aquat. Sci., 66, 1033-1047, 2009.

Stoffels, R.J.: Physiological Trade-Offs Along a Fast-Slow Lifestyle Continuum in Fishes: What Do They Tell Us about Resistance and Resilience to Hypoxia?, PLoS ONE, 10, e0130303, 2015.

Stumm, W., Morgan, J.J.: Aquatic chemistry: an introduction emphasizing chemical equilibria in natural waters, in: Aquatic chemistry: an introduction emphasizing chemical equilibria in natural waters, edited by: Michigan, 795, 1981.

Svendsen, M.B.S., Bushnell, P.G., Christensen, E.A.F., Steffensen, J.F.: Sources of variation in oxygen consumption of aquatic animals demonstrated by simulated constant oxygen consumption and respirometers of different sizes, J. Fish Biol., 88, 51-64, 2016.

Svendsen, M.B.S., Bushnell, P.G., Steffensen, J.F.: Design and setup of intermittent-flow respirometry system for aquatic organisms, J. Fish Biol., 88, 26-50, 2015.

Tanaka, K., Choo, P.-S.: Influences of Nutrient Outwelling from the Mangrove Swamp on the Distribution of Phytoplankton in the Matang Mangrove Estuary, Malaysia, J. Oceanogr., 56, 69-78, 2000.

Thollot, P.: Les poissons de mangrove de Nouvelle-Calédonie: caractérisation du peuplement et relations avec les autres communautés ichtyologiques du lagon, ORSTOM, 52, 1-63, 1989.

Thollot, P.: Importance des mangroves pour la faune ichtyologique des récifs coralliens de Nouvelle-Calédonie, Cybium, 16, 331-344, 1992.

Townsend, S.A., Edwards, C.A.: A fish kill event, hypoxia and other limnological impacts associated with early wet season flow into a lake on the Mary River floodplain, tropical northern Australia, Lakes & Reservoirs: Science, Policy and Management for Sustainable Use, 8, 169-176, 2003.

Tulevech, S.M., Recksiek, C.W.: Acoustic tracking of adult white grunt, Haemulon plumieri, in Puerto Rico and Florida, Fish. Res., 19, 301-319, 1994.

Tyler, R.M., Brady, D.C., Targett, T.E.: Temporal and spatial dynamics of diel-cycling hypoxia in estuarine tributaries, Estuar. Coasts, 32, 123-145, 2009.

Tyler, R.M., Targett, T.E.: Juvenile weakfish Cynoscion regalis distribution in relation to diel-cycling dissolved oxygen in an estuarine tributary, Mar. Ecol. Prog. Ser., 333, 257-269, 2007.

Unsworth, R.K.F., Bell, J.J., Smith, D.J.: Tidal fish connectivity of reef and sea grass habitats in the Indo-Pacific, J. Mar. Biolog. Assoc. U.K., 87, 1287–1296, 2007.

Unsworth, R.K.F., De Leon, P.S., Garrard, S.L., Jompa, J., Smith, D.J.: High connectivity of Indo-Pacific seagrass fish assemblages with mangrove and coral reef habitats, Mar. Ecol. Prog. Ser., 353, 213-224, 2008.

Unsworth, R.K.F., Garrard, S.L., Salinas De León, P., Cullen, L.C., Smith, D.J., Sloman, K.A., Bell, J.J.: Structuring of Indo-Pacific fish assemblages along the mangrove–seagrass continuum, Aquat. Biol., 5, 85-95, 2009.

Van Cappellen, P., Wang, Y.: Cycling of iron and manganese in surface sediments; a general theory for the coupled transport and reaction of carbon, oxygen, nitrogen, sulfur, iron, and manganese, Am. J. Sci., 296, 197-243, 1996.

Vance, D.J., Haywood, M.D.E., Heales, D.S., Kenyon, R.A., Loneragan, N.R., Pendrey, R.C.: How far do prawns and fish move into mangroves? Distribution of juvenile banana prawns *Penaeus merguiensis* and fish in a tropical mangrove forest in northern Australia, Mar. Ecol. Prog. Ser., 131, 115-124, 1996.

Vanderplancke, G., Claireaux, G., Quazuguel, P., Madec, L., Ferraresso, S., Sévère, A., Zambonino-Infante, J.-L., Mazurais, D.: Hypoxic episode during the larval period has long-term effects on European sea bass juveniles (*Dicentrarchus labrax*), Mar. Biol., 162, 367-376, 2015.

Vaquer-Sunyer, R., Duarte, C.M.: Thresholds of hypoxia for marine biodiversity, Proc. Natl. Acad. Sci. U.S.A., 105, 15452-15457, 2008.

Walker, P.: Seasonal and stratigraphic controls in coastal floodplain soils, Soil Res, 10, 127-142, 1972.

Wallace, J., Waltham, N., Burrows, D., McJannet, D.: The temperature regimes of dry-season waterholes in tropical northern Australia: potential effects on fish refugia, Freshw Sci, 34, 663-678, 2015.

Waltham, N.J., Sheaves, M.: Expanding coastal urban and industrial seascape in the Great Barrier Reef World Heritage Area: Critical need for coordinated planning and policy, Mar. Policy, 57, 78-84, 2015.

Wang, S.Y., Lau, K., Lai, K.-P., Zhang, J.-W., Tse, A.C.-K., Li, J.-W., Tong, Y., Chan, T.-F., Wong, C.K.-C., Chiu, J.M.-Y., Au, D.W.-T., Wong, A.S.-T., Kong, R.Y.-C., Wu, R.S.-S.: Hypoxia causes transgenerational impairments in reproduction of fish, Nat. Commun., 7, 12114, 2016.

Wang, T., Lefevre, S., Thanh Huong, D.T., Cong, N.v., Bayley, M.: Chapter 8 The Effects of Hypoxia On Growth and Digestion, 27, 361-396, 2009.

Wannamaker, C.M., Rice, J.A.: Effects of hypoxia on movements and behavior of selected estuarine organisms from the southeastern United States, J. Exp. Mar. Biol. Ecol., 249, 145-163, 2000.

Weinstein, M.P., Litvin, S.Y.: Macro-Restoration of Tidal Wetlands: A Whole Estuary Approach, Ecol. Restor., 34, 27-38, 2016.

Weinstein, M.P., Litvin, S.Y., Guida, V.G.: Considerations of Habitat Linkages, Estuarine Landscapes, and the Trophic Spectrum in Wetland Restoration Design, J. Coast. Res., 51-63, 2005.

Wells, R.M.G.: Chapter 6 Blood-Gas Transport and Hemoglobin Function, in: Fish Physiology: Hypoxia, edited by: Jeffrey G. Richards, Farrell, A.P., Colin, J.B., Academic Press, 255-299, 2009.

White, I., Melville, M.D., Wilson, B.P., Sammut, J.: Reducing acidic discharges from coastal wetlands in eastern Australia, Wetlands Ecol. Manage., 5, 55-72, 1997.

Whitfield, A., Elliott, M.: Fishes as indicators of environmental and ecological changes within estuaries: A review of progress and some suggestions for the future, J. Fish Biol., 61, 229-250, 2002.

Wong, C.C., Drazen, J.C., Callan, C.K., Korsmeyer, K.E.: Hypoxia tolerance in coral-reef triggerfishes (Balistidae), Coral Reefs, 37, 215-225, 2018.

Wood, C.M.: The fallacy of the P_{crit} – are there more useful alternatives?, J. Exp. Biol., 221, jeb163717, 2018.

Wood, S.N. (Eds.): Generalized Additive Models: An Introduction With R, Chapman and Hall/CRC, Florida, 2007.

Wood, S.N.: Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models, J. Roy. Stat. Soc. Ser. B. (Stat. Method.), 73, 3-36, 2011.

Woodroffe, C.: Mangrove Sediments and Geomorphology, in: Tropical Mangrove Ecosystems, edited by: American Geophysical Union, 7-41, 1992.

Wu, R.S.S.: Hypoxia: from molecular responses to ecosystem responses, Mar. Pollut. Bull., 45, 35-45, 2002.

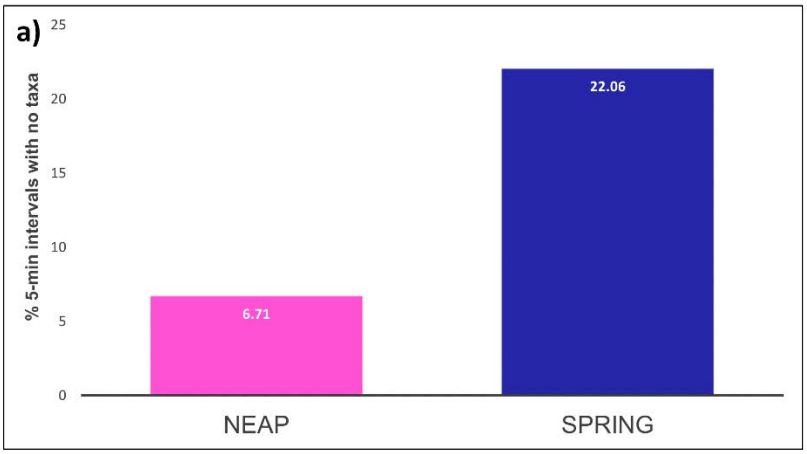
Wu, R.S.S.: Chapter 3 Effects of Hypoxia on Fish Reproduction and Development, in: Fish Physiology: Hypoxia, edited by: Jeffrey G. Richards, Farrell, A.P., Colin, J.B., Academic Press, 79-141, 2009.

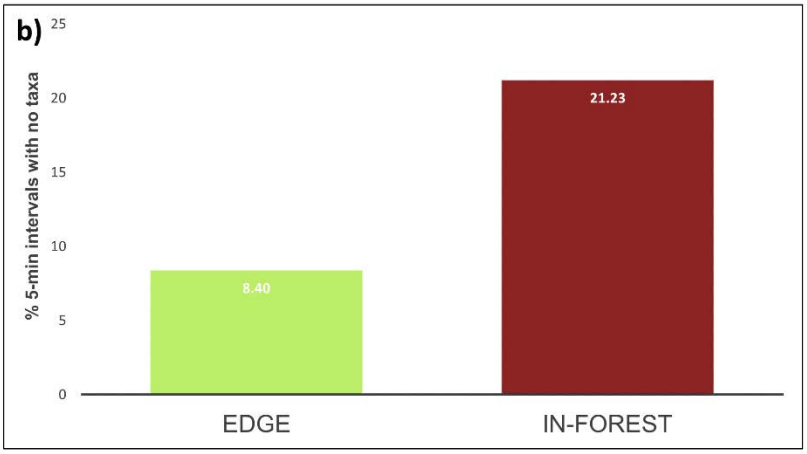
Zambonino-Infante, J.L., Mazurais, D., Dubuc, A., Quéau, P., Vanderplancke, G., Servili, A., Cahu, C., Le Bayon, N., Huelvan, C., Claireaux, G.: An early life hypoxia event has a long-term impact on protein digestion and growth in juvenile European sea bass, J. Exp. Biol., 220, 1846-1851, 2017.

Zuur, A., Ieno, E., Walker, N., Saveliev, A., Smith, G., 2009. Mixed effects models and extensions in ecology with R, , Springer , New York.

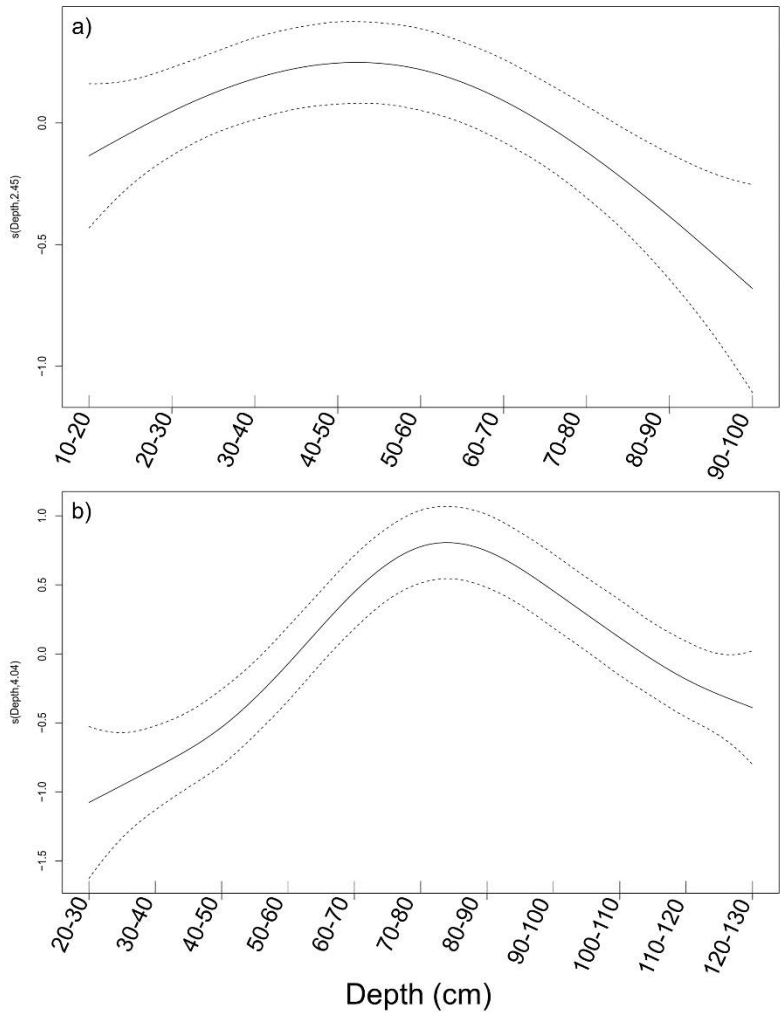
Appendices

S1 Appendix: Dubuc, A. (2019): Dataset: fish assemblages and environmental parameters in Bourake. James Cook University. (dataset). http://doi.org/10.25903/5cd4d312cbcfb

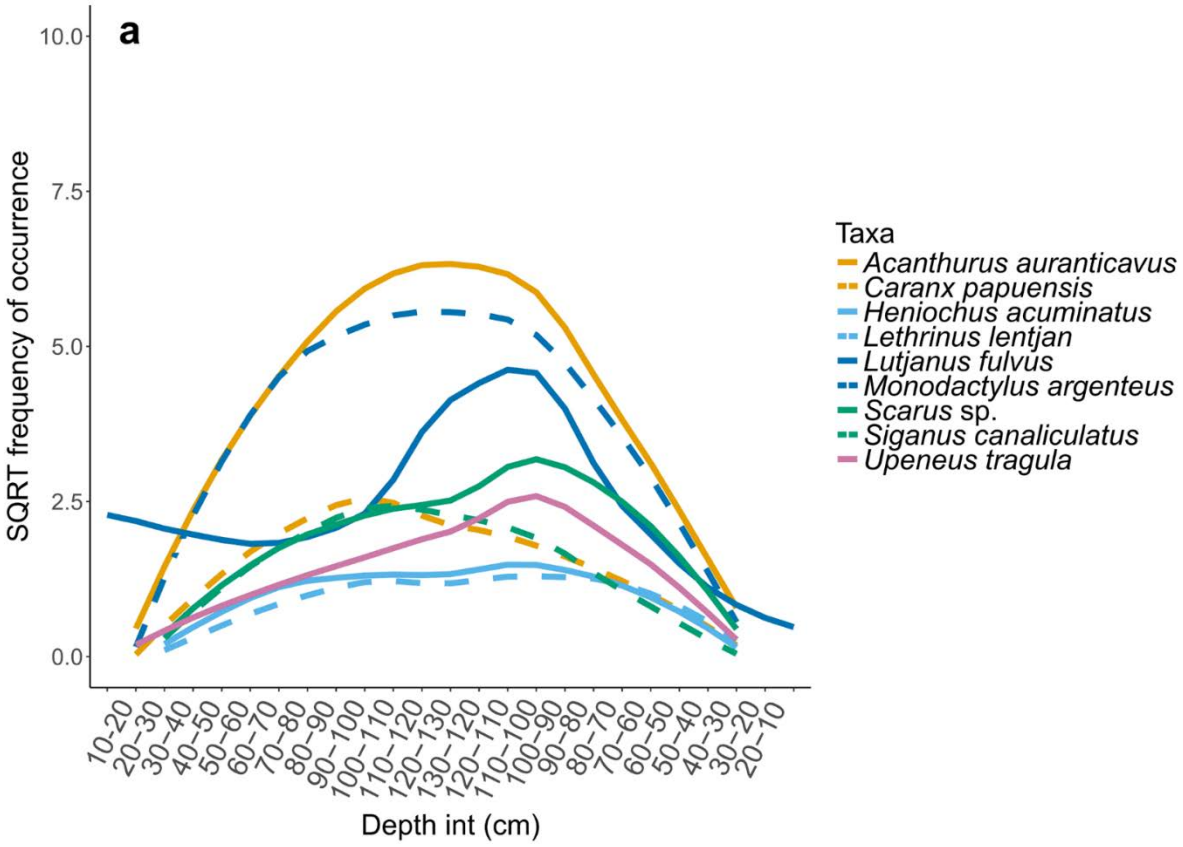


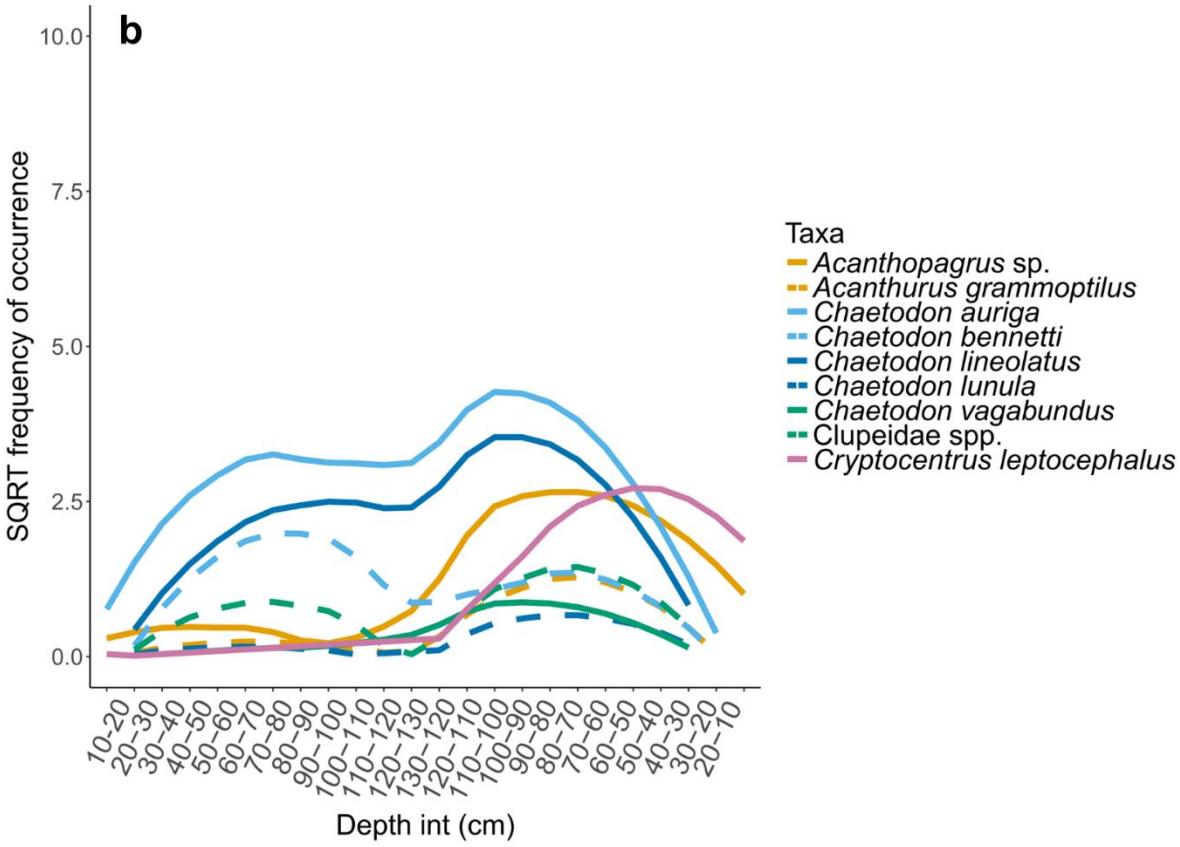


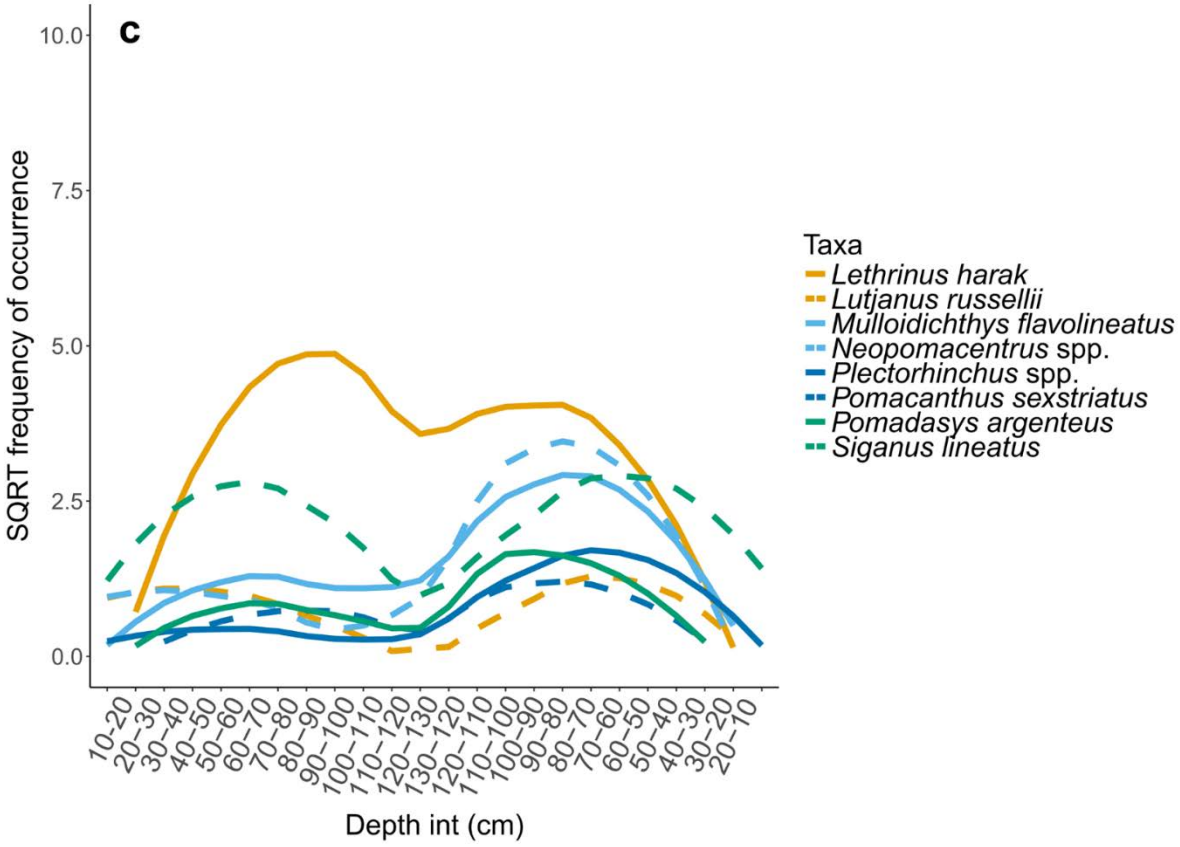
S2 Appendix: Percentage of 5-minutes intervals with no common taxa observed at a) neap tide vs spring tide and b) edge vs in-forest habitats.

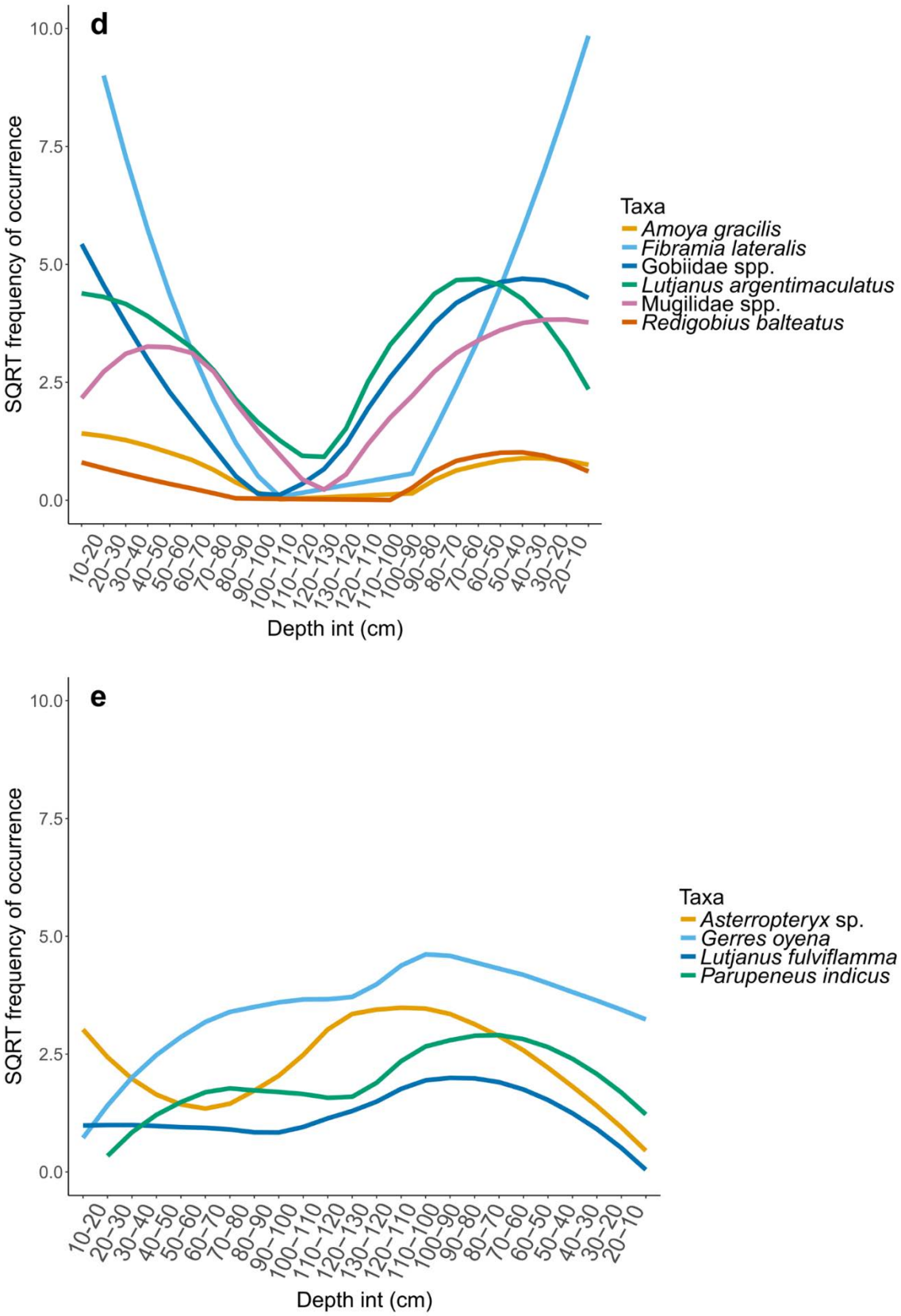


S3 Appendix: General Additive Mixed Model for a) in-forest sites and b) edge sites.

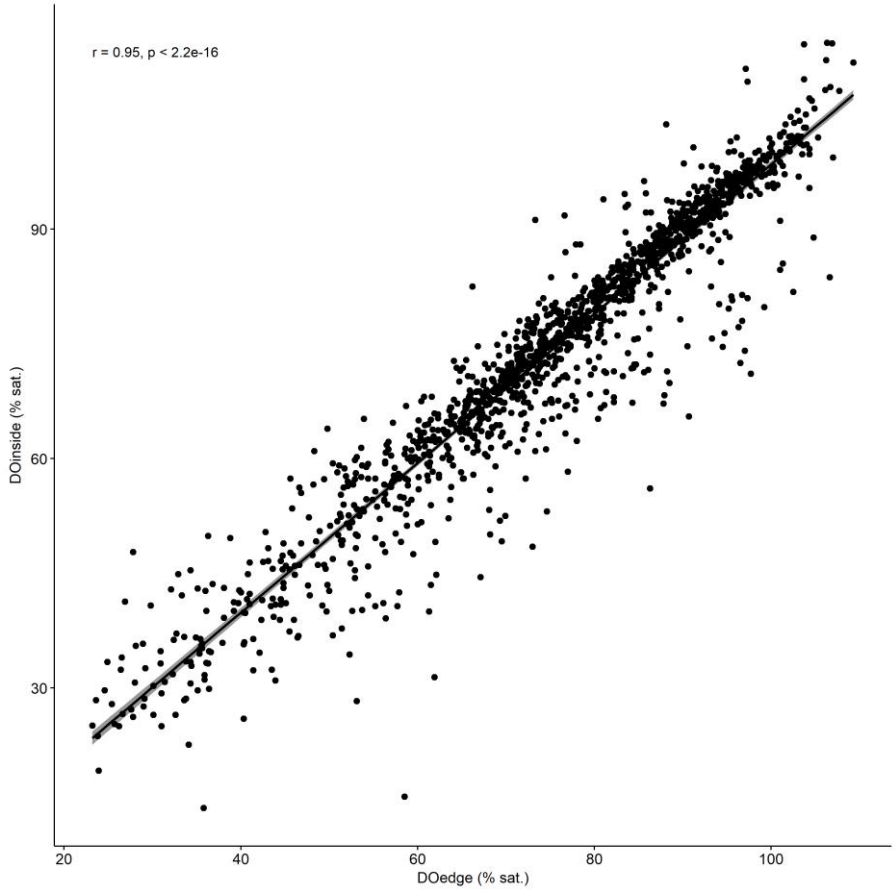

a
10.0
7.5
5.0
2.5
0.0
SQRT frequency of occurrence
10–20
20–30
30–40
40–50
50–60
60–70
70–80
80–90
90–100
100–110
110–120
120–130
130–120
120–110
110–100
100–90
90–80
80–70
70–60
60–50
50–40
40–30
30–20
20–10
Depth int (cm)
Taxa
Acanthurus auranticavus
Caranx papuensis
Heniochus acuminatus
Lethrinus lentjan
Lutjanus fulvus
Monodactylus argenteus
Scarus sp.
Siganus canaliculatus
Upeneus tragula


b
SQRT frequency of occurrence
10.0
7.5
5.0
2.5
0.0
10–20
20–30
30–40
40–50
50–60
60–70
70–80
80–90
90–100
100–110
110–120
120–130
130–120
120–110
110–100
100–90
90–80
80–70
70–60
60–50
50–40
40–30
30–20
20–10
Depth int (cm)
Taxa
Acanthopagrus sp.
Acanthurus grammoptilus
Chaetodon auriga
Chaetodon bennetti
Chaetodon lineolatus
Chaetodon lunula
Chaetodon vagabundus
Clupeidae spp.
Cryptocentrus leptocephalus

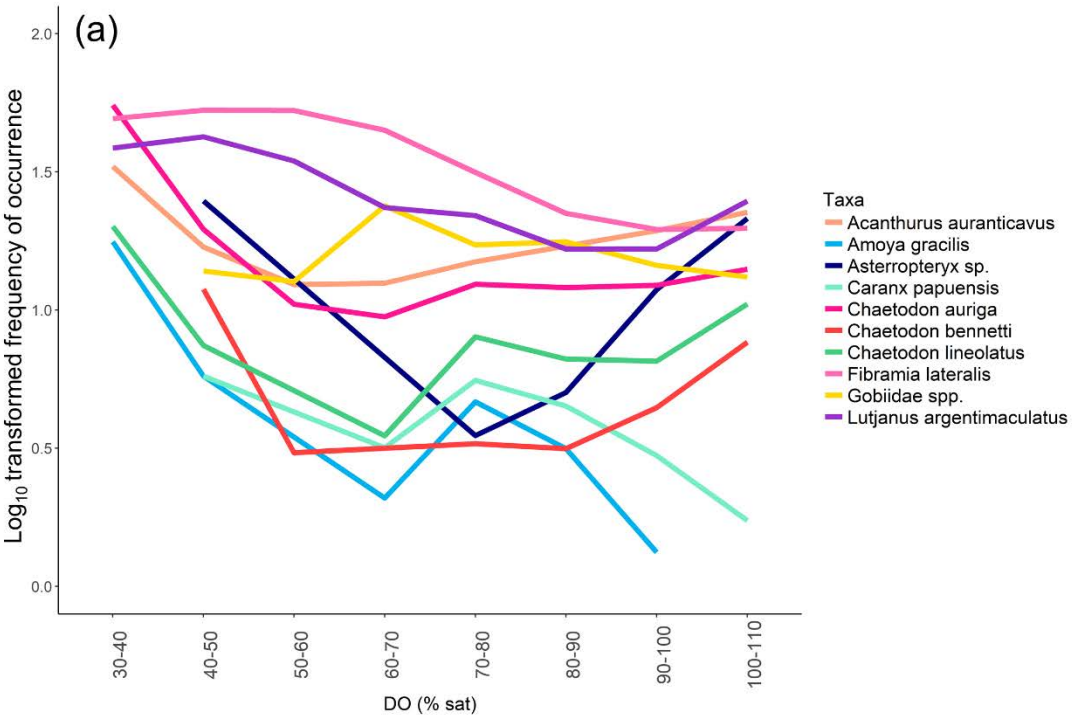

c
SQRT frequency of occurrence
10.0
7.5
5.0
2.5
0.0
10–20
20–30
30–40
40–50
50–60
60–70
70–80
80–90
90–100
100–110
110–120
120–130
130–120
120–110
110–100
100–90
90–80
80–70
70–60
60–50
50–40
40–30
30–20
20–10
Depth int (cm)
Taxa
Lethrinus harak
Lutjanus russellii
Mulloidichthys flavolineatus
Neopomacentrus spp.
Plectorhinchus spp.
Pomacanthus sexstriatus
Pomadasys argenteus
Siganus lineatus

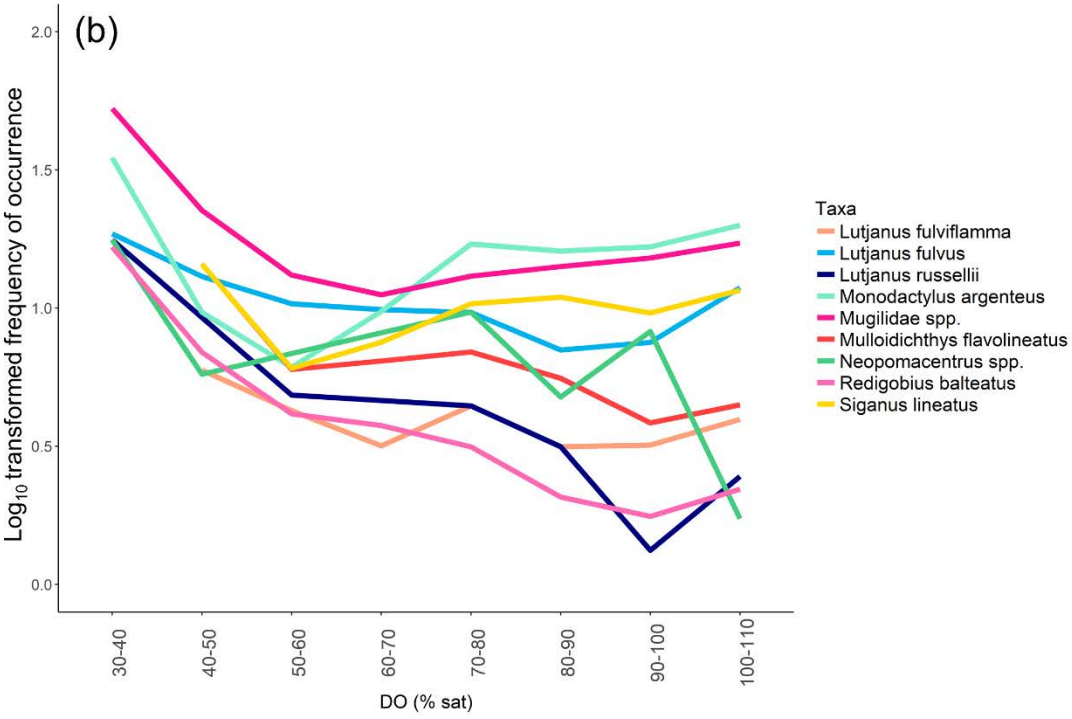


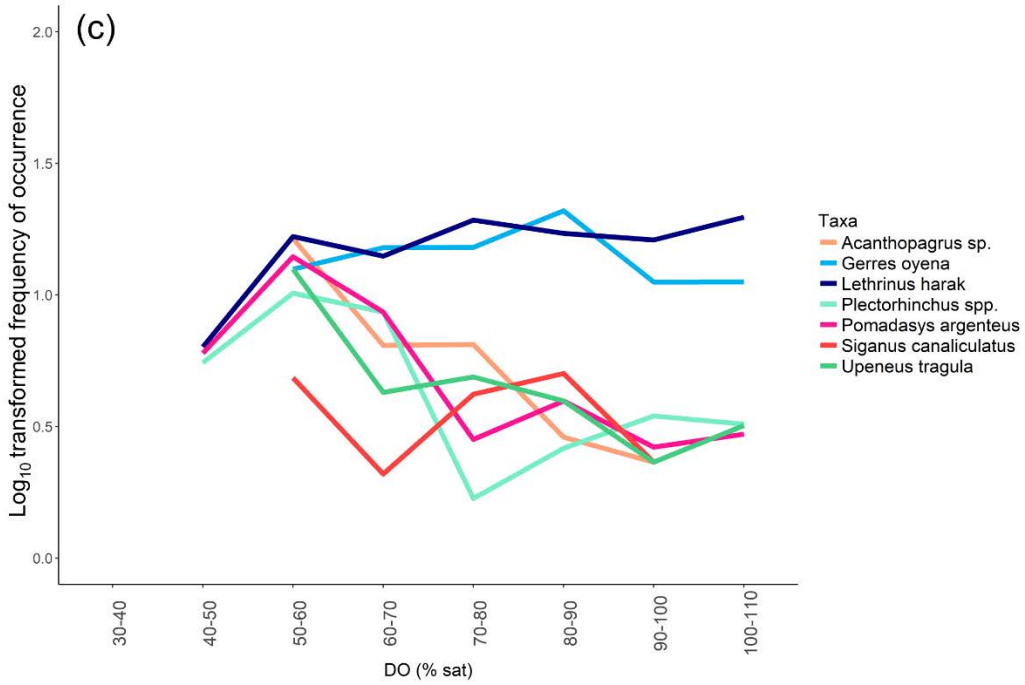
S4 Appendix: Species-specific patterns of mangrove utilisation across depth: a) High-depth users; b) Intermediate-depth users; c) Intermediate-depth users (continued) d) Low-depth users; e) Generalist users.

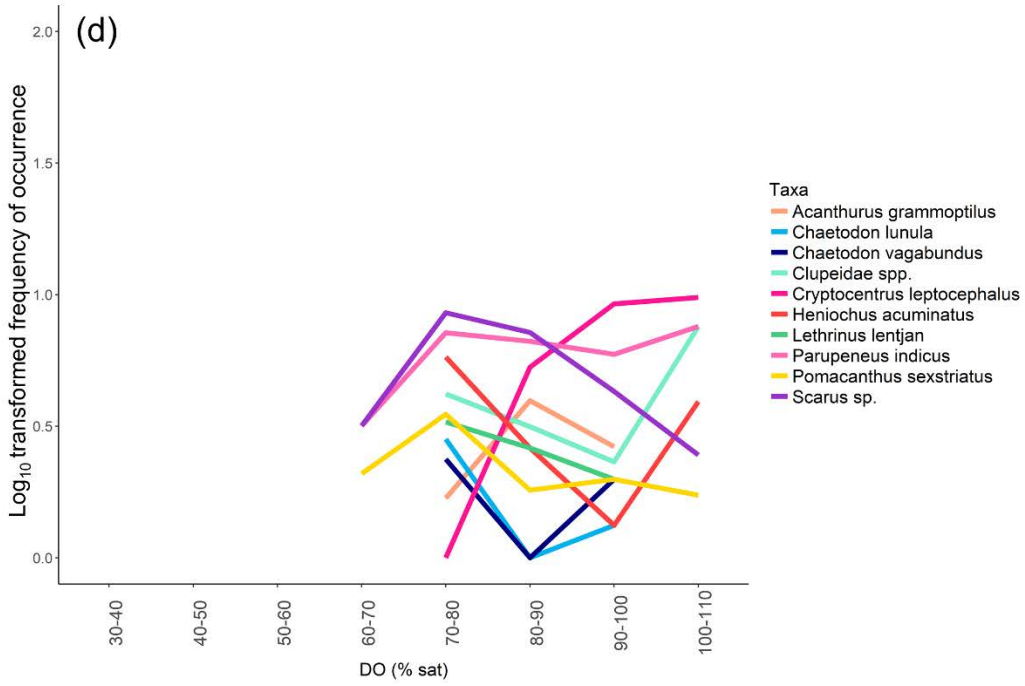


S5 Appendix: Kendall's correlation test used to determine whether patterns of change in DO were significantly correlated between edge and in-forest sites.


(a)
Log10 transformed frequency of occurrence
2.0
1.5
1.0
0.5
0.0
30-40
40-50
50-60
60-70
70-80
80-90
90-100
100-110
DO (% sat)
Taxa
Acanthurus auranticavus
Amoya gracilis
Asterropteryx sp.
Caranx papuensis
Chaetodon auriga
Chaetodon bennetti
Chaetodon lineolatus
Fibramia lateralis
Gobiidae spp.
Lutjanus argentimaculatus


(b)
Log10 transformed frequency of occurrence
2.0
1.5
1.0
0.5
0.0
30-40
40-50
50-60
60-70
70-80
80-90
90-100
100-110
DO (% sat)
Taxa
Lutjanus fulviflamma
Lutjanus fulvus
Lutjanus russellii
Monodactylus argenteus
Mugilidae spp.
Mulloidichthys flavolineatus
Neopomacentrus spp.
Redigobius balteatus
Siganus lineatus





S6 Appendix: Species-specific patterns of mangrove utilisation grouped by type of patterns: (a) Pattern 1: "High tolerance; (b) Pattern 1: "High tolerance" (continued); (c) Pattern 2: "Medium tolerance"; (d) Pattern 3: "Low tolerance".

	Taxonomic richness predicted and corresponding number of 5-min intervals recorded												
Taxonomic richness obs	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
0	**9**	**20**	**25**	**4**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
1	**11**	**13**	**49**	**13**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**
2	**5**	**36**	**93**	**8**	**4**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**
3	**0**	**37**	**69**	**5**	**5**	**0**	**2**	**0**	**0**	**0**	**0**	**0**	**0**
4	**0**	**16**	**36**	**3**	**5**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**
5	**1**	**5**	**22**	**1**	**4**	**0**	**2**	**0**	**0**	**0**	**0**	**0**	**0**
6	**0**	**5**	**13**	**2**	**2**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**
7	**0**	**6**	**7**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
8	**0**	**4**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
9	**0**	**2**	**1**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**
10	**0**	**1**	**3**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
11	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
12	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Total nb of 5-min intervals	**559**												
% exact prediction	**126**	**23**											
% of prediction at +/- 1 taxon	**333**	**60**											

S7 Appendix: Robustness of the random forest model to predict taxonomic richness. The confusion matrix was generated by running the random forest model, built from the training dataset, on the test dataset to identify the percentage of cases when the model was able to predict the exact taxonomic richness observed and the taxonomic richness observed at ± 1 taxon.